FOREST AND WOODLAND STRUCTURE AS AN INDEX OF BIODIVERSITY: A REVIEW

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By Chris McElhinny,
Department of Forestry, Australian National University, Acton Act 0200,
email: chris.mcelhinny@anu.edu.au

Executive summary

The sustainable management of forest and woodland ecosystems requires unambiguous and practical ways of defining and measuring biodiversity. There is an increasing interest in using measures of forest structure for this purpose. To see how this might be achieved, this project reviews the ecological literature concerning the relationship between forest and woodland structure and biodiversity, at the scale of an individual stand. The project is in four parts.

Part one provides a definition of “forest structure”. This is done in terms of “structural attributes”, and “structural complexity”. Structural attributes are broadly defined to include attributes which describe the spatial arrangement of components, the identity and variety of elements, and the types and rates of ecological processes. Structural complexity is considered to be a measure of the number of different attributes present and the relative abundance of each of these attributes.

To identify which attributes might be useful in characterising forest structure parts two and three review relevant international and Australian literature. Part two concludes that relatively few international studies contain extensive sets of structural attributes, and that no single study is likely to provide a definitive suite of attributes. A summary of key structural attributes identified in the international literature is presented in tabular form. Part three reviews Australian studies that have associated the presence, abundance or richness of different faunal groups with various structural attributes. The results are presented under seven major faunal groupings. These attributes are then combined to produce a core set of attributes considered to characterise the habitat requirements of all faunal groups.

To indicate how the structural attributes identified in parts two and three might be combined in a single measure, part four reviews stand level indices of structural complexity. The review indicates that while the literature contains a variety of different indices, no single index can be preferred over the others. The following guidelines are suggested for the development of an index of structural complexity:

1. Use a simple mathematical system to construct the index;
2. Start with a comprehensive set of attributes, which can then be reduced to a core set by establishing relationships between the attributes;
3. Benchmark attributes against their values in natural stands;
4. Trial different weightings of attributes, adopting those weightings which most clearly distinguish between stands.

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Forest and woodland structure as an index of biodiversity – a review

Introduction

Context

The conservation of biodiversity has become a core concern for forest management in both the developing and developed world. This reflects a range of national and international initiatives established following the UN Convention on Biological Diversity, held in Rio de Janeiro 1992 (Grayson and Maynard 1997). These initiatives have committed governments to the maintenance of biodiversity through the sustainable management of forest ecosystems (eg. Commonwealth of Australia 1998).

In order to fulfil such commitments managers require unambiguous and practical ways of defining and measuring biodiversity (Noss 1990). On the basis that biodiversity refers to the diversity of life forms (Hunter 1999), a common approach has been to describe biodiversity in terms of species diversity (Gove 1996, Magurran 1988). However, this has proved problematic because of the variety of different methods used, their lack of agreement with each other (Hurlbert 1971), the impossibility of recording all species (Van Den Meersschaut and Vandekerkhove 1998), and the fact that recording the presence and abundance of different species does not necessarily provide insight as to how to improve management (Stone and Porter 1998).

An alternative approach is to use indicators, or measurable surrogates, to describe and monitor biodiversity (Ferris and Humphrey 1999, Noss 1990). Broadly speaking, biodiversity indicators can be placed into one of two categories, those based on the identification of key species, and those based on the identification of key structures (Lindenmayer *et al.* 2000a). The use of key species has proved problematic because robust relationships between potential indicator species, or groups of species, and total biodiversity have not been well established (Van Den Meersschaut and Vandekerkhove 1998, Lindenmayer and Cunningham 1997).

On the other hand, indicators based on forest structure are generating considerable interest, both in their role as practical surrogates for biodiversity (Uuttera *et al.* 2000, Lahde *et al.* 1999, Koop *et al.* 1994, Buongiorno *et al* 1994) and as a key to understanding the sources of biodiversity in forested ecosystems (Spies 1998, Franklin 1988, Franklin *et al.* 1981). The rationale for utilising measures of structure as surrogate indicators of biodiversity lies in the principle that ecosystems which support a diversity of life forms do so due to the presence of a diversity of resources upon which those life forms depend (Hunter 1999). In forest and woodland environments these resources are often associated with a range of different structural components, including the layering of canopy, decaying logs, hollow bearing trees, the presence of particular understorey species and the availability of trees with different types of bark (Doherty *et al.* 2000). A forest or woodland with a variety of structural components is considered likely to have a variety of resources and species which utilise these resources (Tanabe *et al.* 2001, Brokaw and Lent 1999, Pretzsch 1997, Williams and Woinarski 1997). Consequently there is often a positive correlation between biodiversity and measures of the variety and / or complexity of arrangement of structural components within an ecosystem (MacNally *et al.* 2001).

To be an efficient and effective biodiversity surrogate any measure(s) of structure will need to be based on an appropriate suite of structural attributes. This suite must be sufficiently comprehensive to capture the full range of structural components which occur in forests and woodlands and yet concise enough to function as a practical tool for land managers.

Project aims

Within the context described above this project has two broad aims:

- To review and synthesise international and Australian literature concerning forest and woodland structure and its relationship to biodiversity;
- To identify a suitable suite of attributes with which to characterise the structure of Australian forests and woodlands at the scale of a stand;

Approach

The project addresses these aims in four stages:

PART ONE: defines the terms “forest structure”, “structural attribute”, and “structural complexity”;

PART TWO: reviews the international literature concerning attributes of forest structure which have been used as surrogates for biodiversity.

PART THREE: identifies a core set of attributes suitable for characterising the stand level structure of temperate forests and woodlands in Australia. This is achieved by reviewing studies of Australian ecosystems, which have associated the presence, abundance or richness of different faunal groups with various vegetation attributes. The results are presented under seven major faunal groupings.

PART FOUR: concludes the project by reviewing stand level indices of structural complexity, which summarise two or more structural attributes in a single measure.

1. Defining forest structure

1.1 Ecosystem structure, function and composition

Ecosystems are frequently characterised in terms of their species and genetic composition (Hunter 1999), even though this approach ignores ecological processes (eg. natural disturbance, the decomposition of woody debris, the cycling of nutrients etc.), which are critical for the maintenance of biodiversity (Noss 1990). An alternative approach, first suggested more than two decades ago, (eg. Franklin *et al.* 1981), is to describe forest ecosystems by attributes relating to ecosystem structure and function in addition to those describing composition (Franklin *et al.* 2002, Noss 1990, Franklin 1988). In this approach:

- *Structure* refers to the spatial arrangement of the various components of the ecosystem, such as the heights of different canopy levels and the spacing of trees;
- *Function* refers to how various ecological processes, such as the production of organic matter, are accomplished and to the rates at which they occur;
- *Composition* refers to the identity and variety of elements, as characterised by species richness and abundance.

These three attribute groupings operate over a range of scales from landscape to individual. Noss (1990) used these scales to arrange the attribute groupings into a nested hierarchy, in which organisation at the scale of species or populations provided the basis for many larger scale patterns. While this approach does not imply that there is a single scale of organisation which is fundamental to the maintenance of biodiversity, it does highlight the importance of attributes and variation at a local, or stand[1] scale (Noss 1999). The stand is also the scale at which management decisions are usually implemented so that the outcome of monitoring attributes at this scale is more likely to translate into improved practices (O'Hara 1998). While acknowledging the importance of landscape attributes, the focus for this review will therefore be at the scale of an individual stand.

1.2 Structural attributes

The structural, functional and compositional attributes of a stand are often interdependent, so that attributes from one group may also be a surrogate for attributes from another group (Franklin *et al.* 2002, Ferris and Humphrey 1999,

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[1] A stand is an area of forest or woodland with a relatively uniform structure, and which can be managed as a single unit.

Noss 1990). For example a structural attribute such as dead wood may also be a good indicator of functional attributes such as decomposition and nutrient cycling processes. Similarly compositional attributes, such as species composition and abundance can be indicators of structural attributes such as hollow bearing trees, or of functional attributes such as flowering and bark shedding (Franklin *et al.* 2002, Kavanagh 1987). The division of attributes into three groupings is by no means a clear and distinct categorisation. In order to define structure in an unambiguous manner I will therefore pool structural, functional and compositional attributes into a single category simply called structural attributes. Landscape structure or stand structure will refer to the pattern of organisation of these attributes at a particular scale.

1.3 Stand structure

For the purposes of this review stand structure will be defined in terms of two components - stand level structural attributes and stand structural complexity[2]. Stand level structural attributes can include measures of:

- Abundance - eg. density of large trees (Acker *et al.* 1998), volume of dead wood (Wickstrom and Erickson 2000);
- Relative abundance - eg. foliage height diversity (MacArthur and MacArthur 1961), dbh diversity (Gove 1996, Buongiorno *et al.* 1994), basal area of deciduous tree species (Spies and Franklin 1991).
- Richness - eg. overstorey species richness (Munks *et al.* 1996), eucalypt species richness (Bauer *et al.* 2000), shrub species richness (Seddon *et al.* 2001);
- Size variation - eg. standard deviation of dbh (Spies and Franklin 1991);
- Spatial variation - eg. coefficient of variation of distance to nearest neighbour (Franklin *et al.* 1981);

Attributes that quantify variation are particularly important because these can also describe habitat heterogeneity at the stand scale. For example the coefficient of variation of shrub cover would be a measure of the patchiness of understorey vegetation, a feature which is important for some species of macropod (Lunney and Ashby 1987).

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[2] In this review "structural complexity" is used in preference to "structural diversity" because the latter term is considered ambiguous. This reflects the work of a number of authors in which a diversity measure, such as the Shannon-Weiner Index, is used to quantify a single attribute, such as variation in stem diameter (eg. Gove *et al.* 1995, Buongiorno *et al.* 1994). This quantity is then deemed a measure of structural diversity and to be indicative of biological diversity. In reality all that has been quantified is one of many possible attributes, and by most measures of diversity a system with one attribute or element has a diversity of zero (Magurran 1988).

Stand structural complexity is essentially a measure of the number of different attributes present and the relative abundance of each of these attributes. Structural complexity therefore involves the interaction of a number of different variables (attributes) so that quantitative comparisons between stands can require complex multivariate analysis (eg. Spies and Franklin 1991). In response to this problem, a variety of indices have been devised which aim to express structural complexity as a single number, thereby facilitating comparisons between stands (eg. Koop *et al.* 1994, Newsome and Catling 1979). By acting as a summary variable for a larger pool of structural attributes these indices can also provide a means of ranking stands in terms of their potential contribution to biodiversity (eg. Van Den Meersschaut and Vandekerkhove 1998).

Constructing an index of structural complexity involves deciding on the type and number of attributes to be used and their relative weighting in the calculation of the index. To shed light on how this might be done I will review the international and Australian literature to:

a) Identify the range of stand level attributes that have been used to characterise biodiversity;

b) Critique existing indices of stand structural complexity.

I shall start with a review of stand level attributes as they appear in the international literature.

2. Stand level attributes – an international review

2.1 Overview of attributes

A variety of different attributes has been used in the international literature to characterise stand structure. These attributes, and associated studies are summarised in Table 1. Of the studies, only a handful contains extensive sets of attributes (eg. Van Den Meersschaut and Vandekerkhove 1998, Spies and Franklin 1991, Franklin *et al.* 1981), none of which is likely to provide a definitive suite of attributes capable of characterising the full biodiversity potential of a stand. However it is hoped that by considering attributes across a range of studies (Table 1) some insight may be gained into this problem. For clarity, attributes have been grouped in Table 1 under the stand element which they aim to describe (eg. foliage, tree diameter etc.). For studies where a large number of attributes were tested, only those attributes which proved significant in the modelling process have been included in Table 1. In the following sections, the relevance of each stand element and its associated attributes are discussed in more detail.

Table 1: Attributes which have been used to characterise stand structure in the international literature. Attributes are grouped under the stand element they aim to describe

Stand element	Attribute	Source
Foliage	Foliage Height Diversity	Sullivan *et al.* 2001, Tanabe *et al.* 2001, Berger and Puettmann 2000, Gove 1996, MacArthur and MacArthur 1961
	Number of strata	Tanabe *et al.* 2001, Van Den Meersschaut *et al.* 1998, Maltamo *et al.* 1997, Uuttera *et al.* 1997, Koop *et al.* 1994, MacArthur and MacArthur 1961
	Foliage density within different strata	Bebi *et al.* 2001, Ferris-Kaan *et al.* 1996
Canopy cover	Canopy cover	Van Den Meersschaut *et al.* 1998
	Gap size classes	Tyrell and Crow 1994
	Average gap size and the proportion of canopy in gaps	Tanabe *et al.* 2001, Ziegler 2000, Tyrell and Crow 1994
	Proportion of tree crowns with broken and dead tops	Spies and Franklin 1991
Tree diameter	Tree DBH	Tanabe *et al.* 2001, Ziegler 2000, Ferreira *et al.* 1999, Uuttera *et al.* 1997, Acker *et al.* 1998, Spies and Franklin 1991
	Standard deviation of DBH (coefficient of variation[A])	Zenner 2000, Acker *et al.* 1998, Van Den Meersschaut *et al.* 1998, Spies and Franklin 1991, Franklin *et al.* 1981[A]
	Tree size diversity	Wikstrom and Erickson 2000, Gove 1996, Buongiorno *et al.* 1994
	Horizontal variation in DBH	Zenner 2000
	Diameter distribution	Bachofen and Zingg 2001, Uuttera *et al.* 2000, Ferreira *et al.* 1999, Maltamo *et al.* 1997, Kappelle *et al.* 1996, Tyrell and Crow 1994, Koop *et al.* 1994
	Number of large trees	Ziegler 2000, Acker *et al.* 1998, Van Den Meersschaut *et al.* 1998, Tyrell and Crow 1994, Koop *et al.* 1994, Spies and Franklin 1991
Tree height	Height of overstorey	Bebi *et al.* 2001, Means *et al.* 1999, Spies 1998, Kappelle *et al.* 1996, Koop *et al.* 1994
	Standard deviation of tree height	Zenner 2000
	Horizontal variation in height	Svennson and Jeglum 2001, Zenner 2000
	Height class richness	Sullivan *et al.* 2001
Tree spacing	Clark Evans Index, Cox Index[B], percentage of trees in clusters[C]	Bachofen and Zingg 2001, Svensson and Jeglum 2001[B], Bebi *et al.* 2001[C], Zenner 2000, Pretzsch 1997
	Number of trees per ha	Bachofen and Zingg 2001, Uuttera *et al.* 2000, Ferreira *et al.* 1999, Acker *et al.* 1998, Kappelle *et al.* 1996, Spies and Franklin 1991
Stand biomass	Stand basal area	Berger and Puettmann 2000, Ziegler 2000, Means *et al.* 1999, Ferreira *et al.* 1999, Kappelle *et al.* 1996, Koop *et al.* 1994
	Stand volume	Uuttera *et al.* 2000, Means *et al.* 1999, Ferreira *et al.* 1999, Spies 1998
Tree species	Species diversity and / or richness	Sullivan *et al.* 2001, Uuttera *et al.* 2000, Van Den Meersschaut *et al.* 1998, Maltamo *et al.* 1997, Uuttera *et al.* 1997,
	Relative abundance of key species	Ziegler 2000, Wikstrom and Erickson 2000, Spies and Franklin 1991
Understorey vegetation	Herbaceous cover and its variation	Van Den Meersschaut *et al.* 1998, Spies and Franklin 1991
	Shrub cover	Berger and Puettmann 2000, Spies and Franklin 1991
	Shrub height	Berger and Puettmann 2000
	Total cover of understorey	Spies and Franklin 1991
	Understorey richness	Sullivan *et al.* 2001, Van Den Meersschaut *et al.* 1998
	Saplings (shade tolerant[D]) per ha	Van Den Meersschaut *et al.* 1998, Spies and Franklin 1991[D]
Dead wood	Number, volume or basal area[E] of stags (by decay classes[F], by diameter class[G])	Bachofen and Zingg 2001, Svennson and Jeglum 2001[G], Sullivan *et al.* 2001, Van Den Meersschaut *et al.* 1998[E], Tyrell and Crow 1994[E], Spies and Franklin 1991[F], Franklin *et al.* 1981[F]
	Volume of coarse woody debris	Sullivan *et al.* 2001, Svennson and Jeglum 2001, Ziegler *et al.* 2000, Wikstrom and Erickson 2000, Tyrell and Crow 1994
	Log volume by decay or diameter[H] classes	Van Den Meersschaut *et al.* 1998[H]. Tyrell and Crow 1994, Spies and Franklin 1991, Franklin *et al.* 1981
	Coefficient of variation of log density	Spies and Franklin (1991)

2.2 Foliage

The vertical arrangement of foliage is a common attribute used in the literature to describe stand structure (Brokaw and Lent 1999), and the first in which a quantitative relationship was established between an element of structure and a measure of faunal diversity. In a landmark study, MacArthur and MacArthur (1961) established a linear relationship between their new measure Foliage Height Diversity (FHD), which described the arrangement of foliage within different vertical strata, and Bird Species Diversity (BSD). FHD was based on an index developed by communications engineers, and was defined by the relationship $FHD = -\sum p_i \ln p_i$; where p_i is the proportion of total foliage which lies in the ith of the chosen foliage layers. BSD was described using a similar approach where $BSD = -\sum p_i \ln p_i$; and p_i is the proportion of all bird individuals which belong to the ith species.

By a process of trial and error MacArthur and MacArthur (1961) found that the three height classes 0-2', 2'-25' and >25' gave the best correlation between BSD and FHD. These divisions also corresponded to the layers occupied by the foliage of herbs, shrubs and trees respectively. The authors concluded that it was the distribution of foliage amongst different lifeforms which provided more kinds of habitat and thereby supported a greater diversity of birds.

MacArthur and MacArthur's results have been supported by a number of subsequent studies (Ambuel and Temple 1983, Abbott 1976, Recher 1969). This has encouraged the use of FHD as a measure of forest structure and its acceptance by some authors as a reliable indicator of biodiversity (Tanabe at al 2001, Gove 1996, Buongiorno *et al.* 1994), - although there is little evidence to suggest that FHD can explain differences in the diversity of faunal groups other than birds.

Despite its acceptance by some authors, FHD appears as an ambiguous measure in the literature with no standard method established for its measurement. When calculating FHD different studies have assessed vegetation density in different ways (Parker and Brown 2000, Erdelen 1984), and unlike MacArthur and MacArthur's original study in which class intervals related to distinct strata, the delineation of height classes is often arbitrary (eg. Sullivan *et al.* 2001, Tanabe *et al.* 2001). The precision of these various approaches and their correlation with each other is unclear and limits comparisons between studies (Erdelen 1984).

Alternatives to FHD as measures of foliage structure include:

- Comparing foliage cover for selected species in selected strata (Bebi *et al.* 2001) or comparing the relative cover for selected species in two strata, eg. the ratio of lower canopy cover to field layer cover (Ferris-Kaan *et al.* 1996);
- Specifying the number of strata on the basis that multi-layered stands increase the diversity of habitat niches (Van Den Meersschaut and Vandekerkhove 1998);

Both of these approaches assume that the strata within a canopy can be clearly and consistently defined. Parker and Brown (2000) indicated that this is unlikely to be the case. They reviewed the concept of "canopy stratification" in the ecological literature, and demonstrated that the term had a variety of meanings that were both difficult to measure and to reconcile. As a practical demonstration of this ambiguity they applied a variety of definitions of stratification to a mixed-oak forest canopy in south-western Virginia, USA. These definitions failed to consistently and clearly identify the presence, number or location of strata. They suggest it would be more meaningful to define strata in terms of the ecological gradients created by foliage (eg. changes in light transmittance levels) rather than attempt to describe the arrangement of the foliage itself.

The use of attributes of vertical foliage arrangement to characterise stand structure would therefore appear more common than sensible. A related but more straightforward approach has been to characterise structure in terms of canopy cover and the variation in that cover produced by canopy gaps.

2.3 Canopy cover

Canopy cover has been described as one of the most important characteristics of forest structure, and at a stand level it can be used to characterise stand productivity and the distribution and abundance of biomass (Burgman and Lindenmayer 1998). Canopy cover is commonly defined as the percentage cover of the vertical projection of tree crowns, where the crowns are considered as opaque objects (Walker and Hopkins 1990).

Distinct changes have been observed in canopy cover during stand development. For example in an even-aged stand canopy cover will generally increase from a low level at stand initiation, reaching a maximum at the stem exclusion stage, then declining as overstorey elements disintegrate and canopy gaps form during the old-growth stage (Franklin *et al.* 2002, Oliver and Larsen

1996). Van Den Meersschaut and Vandekerkhove (1998) acknowledged this dynamic when quantifying canopy cover as a component of an index of forest structure for closed forests in Belgium. They gave the maximum score in their index for stands with 1/3 to 2/3 canopy cover.

A number of studies have confirmed the importance of canopy gaps as attributes of canopy cover. In North America, Ziegler (2000) and Tyrrell and Crow (1994) found that the proportion of the canopy in gaps, the average size of gaps and the distribution of gaps amongst size classes were all important attributes for distinguishing old-growth hemlock (*Tsuga canadensis* (L.) Carr.) hardwood forests from earlier successional stages. Similarly, Spies and Franklin (1991) found that the number of trees with dead tops or broken crowns was a key attribute that distinguished between old-growth, mature and young stands in Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) forests.

While the extent and condition of canopy cover are clearly important attributes of forest structure they appear relatively infrequently in the literature. The overwhelming focus for most studies has been the use of attributes related to the size of tree stems such as tree diameter, height and volume. This in part reflects the association between stem size and other structural attributes such as foliage distribution, crown dimensions and the production of dead wood of different sizes (Spies 1998). It also reflects the fact that data on stem size are relatively straightforward to collect and have historically formed the basis of many permanent plot measurements.

2.4 Tree diameter

Tree diameter is the most ubiquitous measure of tree size in the literature concerning forest structure, and it is typically quantified in terms of mean tree dbh, the standard deviation of tree dbh and the number of trees exceeding a threshold diameter (ie the number of large trees). Spies and Franklin (1991) identified these three attributes as amongst the most important for characterising wildlife habitat, ecosystem function and successional development in Douglas-fir forests.

Mean dbh generally increases with stand age and has been used to discriminate between successional stages in Douglas-fir forests (Spies and Franklin 1991), hemlock-hardwood forests (Ziegler 2000) and between managed and virgin boreal forests in Finnish and Russian Karelia (Uuttera *et al.* 1997). However Franklin *et al.* (1981) found that old-growth and young stands of Douglas-fir had a similar mean dbh, although the old-growth stand had nearly twice the coefficient of variation in dbh compared to the young stand.

Stand basal area is an attribute which is directly related to mean dbh. It is also indicative of stand volume and biomass. Stand basal area has been used to discriminate between primary and secondary *Quercus* forest in Costa Rica (Kappelle *et al.* 1996), and successional stages in hemlock-hardwood forests (Ziegler 2000). Berger and Peutmann (2000) found that stand basal area was important in explaining differences in herbaceous plant diversity which occurred between three types of aspen-conifer forest.

<u>The standard deviation of tree dbh</u> is a measure of the variability in tree size, and is considered indicative of the diversity of micro-habitats within a stand (Acker *et al.* 1998, Van Den Meerschautt and Vandekerkhove 1998). It is a straightforward attribute to quantify and can be comparable to more complex attributes and indices as a descriptor of stand structure (Neumann and Starlinger 2001). For example Spies and Franklin (1991) found that the standard deviation of dbh was more useful than a measure of height diversity in discriminating between successional stages of Douglas-fir forests. Similarly, Zenner (2000) found that a Structural Complexity Index based on a three dimensional model of forest structure was significantly correlated with the standard deviation of dbh, and Neumann *et al.* (2001) found that the standard deviation of dbh was significantly correlated with 7 indices of structural complexity they tested.

<u>The number of large trees</u> is indicative of the potential number of stags, downed logs and hollow bearing trees, all of which provide important habitat resources for arthropods, birds and mammals (Acker *et al.* 1998). Large trees have also been associated with four key structural attributes distinguishing old-growth Douglas-fir forests from earlier successional stages. Franklin *et al.* (1981) identified these as:
1. Large living old-growth trees with dbh >100 cm;
2. Large dead standing trees;
3. Large logs on land and;
4. Large logs in streams.

The number of large trees has been used to characterise the structure of hemlock-hardwood stands (Ziegler 2000, Tyrrell and Crow 1994), Douglas-fir stands (Aker *et al.* 1998, Spies and Franklin 1991, Franklin *et al.* 1981) temperate forests in Belgium (Van Den Meerschaut and Vandekerkhove 1998) and Sumatran rainforest (Koop *et al.* 1994). The threshold diameter used to define a large tree varies between these studies, ranging from > 70 cm in the case of Tyrrell and Crow (1994) to > 100 cm dbh in the case of Spies and Franklin (1991). The ecological basis for these thresholds is unclear, although they presumably reflect potential growth over a time frame required for individual trees to become mature and over-mature.

Quantifying the number of large trees essentially places trees into two diameter classes. A number of different authors have taken the next logical step of using a diameter distribution across a range of diameter classes as an attribute of stand structure. Koop *et al.* (1994) applied this approach in a simple form. Stands with a reverse J distribution, indicative of uneven-aged stands, scored 2 points on an index of structure, whereas any other distribution scored 1 point. A more elaborate approach was adopted by Tyrell and Crow (1994), who compared tree numbers across 10 cm diameter classes to characterise the structure of hemlock-hardwood stands. They found that old-growth stands were distinguished by a relatively even diameter distribution, with low densities of trees across all diameter classes.

This contrasts with a number of studies in tropical forests in which diameter distribution did not appear as a particularly useful or significant attribute with which to characterise forest structure (Uuttera *et al.* 2000, Ferreira *et al.* 1999, Kappelle *et al.* 1996). In these forests, management often removes large trees of commercial species, so that changes in structure may be better characterised by assessing a few species in particular diameter classes rather than the entire diameter distribution (Uuttera *et al.* 2000).

One of the drawbacks to using diameter distribution as an attribute of forest structure is the complexity of comparing distributions from different stands. A number of authors have therefore used the Shannon-Weiner Index to summarise stand diameter distribution in a single measure called tree size diversity (H'); where,$H' = -\sum (p_i \ln p_i)$; and p_i is the proportion of trees in the ith diameter class (Wikstrom and Erickson 2000, Gove 1996, Buongiorno *et al.* 1994). This measure permits direct comparisons between diameter distributions, and also provides a simple attribute which can be modelled under different management strategies. For example Buongiorno *et al.* (1994) modelled the relationship between tree size diversity and sustainable timber revenue in northern hardwood stands in Wisconsin, USA.

The validity of using tree size diversity as an attribute of structure is not clearly established in the literature. Buongiorno *et al.* (1994) claim tree size diversity to be a good proxy for foliage height diversity, on the basis that a diversity of tree sizes will equate with a diversity of canopy heights and foliage arrangements. However this argument is flawed; firstly because it could only apply in forests containing shade tolerant species which can form lower strata; and secondly because foliage height diversity is sensitive to the way in which height classes are defined (Parker and Brown 2000). MacArthur and MacArthur (1961) used unequal height classes which equated to distinct canopy strata. Tree size diversity on the other hand establishes arbitrary classes based on equal diameter class widths rather than observable strata.

In contrast to Buongiorno *et al.* (1994), Gove (1996) drew no connection between foliage height diversity and tree size diversity. Instead, Gove (1996) used these measures to characterise different attributes of the structure of Spruce-Fir stands in Maine. Foliage height diversity was used to characterise vertical structure and tree size diversity was used to characterise horizontal structure. However, as Zenner (2000) demonstrates, stands with the same diameter distribution - and hence tree size diversity - can have trees in very different spatial arrangements. It would therefore appear that the use of tree size diversity as a structural attribute has more to do with it being a quantity which is easy to compute and model rather than with any established connection to stand structure or biodiversity.

2.5 Tree height

Quantitative relationships between tree height and diameter are well established in the literature (Martin and Flewelling 1998), so that to some extent structural attributes associated with diameter may also serve as proxies for attributes associated with tree height (eg. Buongiorno *et al.* 1994). However, because the relationship between height and diameter is non-linear it is often more meaningful to use attributes directly associated with height when characterising vertical elements of structure. For example the standard deviation of tree height will be more indicative of the vertical layering of foliage than the standard deviation of dbh (Zenner 2000).

The simplest attribute associated with height is the height of the overstorey. It is an attribute, which is readily derived from remotely sensed data (eg. Bebi *et al.* 2001, Means *et al.* 1999), and is considered indicative of successional stage (Kappelle *et al.* 1996), the number of strata (Spies 1998) and stand biomass

(Means *et al.* 1999).

Variation in tree height is considered an important attribute of structure because stands containing a variety of tree heights are also likely to contain a variety of tree ages and species thereby providing a diversity of micro-habitats for wildlife (Zenner 2000). Sullivan *et al.* (2001) quantified this type of variation in terms of a simple measure called structural richness, which was based on the number of height classes occupied by the trees in the stand.

Zenner (2000) and Svensson and Jeglum (2001) indicate that variation in tree height is more complex than structural richness, because it depends on the horizontal arrangement of the trees as well as the height of the trees. Zenner (2000) therefore used a three dimensional model of the position of trees to describe variation in tree height in terms of a structural complexity index. This index is discussed in section 4.4.

2.6 Tree spacing

In contrast to the approach of Zenner (2000), a number of authors have used the horizontal distribution of trees as a structural attribute in its own right. The simplest way to do this is to use the number of trees per ha as a measure of the average space between trees. This attribute has successfully distinguished between successional stages of unmanaged Douglas-fir forests (Spies and Franklin 1991), and primary and secondary tropical forest in central Amazonia (Ferreira *et al.* 1999). However a number of other studies in tropical forest systems have not confirmed that number of stems per ha is a useful attribute, and in these forests it failed to distinguish between the structure of primary and secondary forest (Uuttera *et al.* 2000, Kappelle *et al.* 1996).

A more complex approach is to describe tree spacing in terms of its variation rather than its average dimension. This is likely to be more meaningful because it is indicative of the size and distribution of gaps, and these are critical to processes such as recruitment, competition and mortality (Svensson and Jeglum 2001). Typically variation in spacing is described by an aggregation index which quantifies the degree of clustering in the horizontal arrangement of trees (Neumann and Starlinger 2001).

A common index used for this purpose is the Clark Evans aggregation index (Pretzsch 1997). This index describes the ratio between the observed average distance of a tree to its nearest neighbour and the expected average distance for a random tree distribution. Aggregation values below 1 are indicative of a tendency towards clustering, values close to 1 indicate a random distribution and values greater than 1 are indicative of an increasingly regular distribution (Clark and Evans 1954). Bachofen and Zingg (2001) found that the Clark-Evans index was one of the three most useful attributes for detecting structural changes in subalpine Norway Spruce forests. The main problem with applying this index is that it requires nearest neighbour distances to be determined for each tree in the plot.

The Cox Index of clumping addresses this issue, by quantifying the variance to mean ratio of the number of trees in equal sized sub-plots, rather than using nearest neighbour distances (Cox 1971 cited in Neumann *et al.* 2001). A variance to mean ratio of 1 indicates a random distribution, values less than 1 a regular distribution and values greater than 1 an increasingly clustered distribution. Svensson and Jeglum (2001) applied the variance to mean ratio approach to an undisturbed old-growth Norway Spruce forest. They found a clear difference between the spatial distribution of the overstorey and understorey trees. Trees in the overstorey were randomly distributed whereas trees in the understorey were clumped. The clumping reflected the location of understorey trees in the spaces between overstorey trees. The authors concluded that a key characteristic of old-growth Norway Spruce forest was a disorderly three dimensional structure and that this was well described by the variance to mean ratio of tree numbers (Svensson and Jeglum 2001). Franklin *et al.* (1981) described a similar effect in old-growth Douglas-fir forests in which groups of small diameter shade tolerant trees developed under an overstorey of large well spaced Douglas-firs.

2.7 Tree species

Many of the attributes which have been described in the preceding sections can be related in some degree to the presence of a variety of tree species. For example the presence of a mix of shade tolerant and shade intolerant tree species is likely to produce a multi-layered canopy, a large variety of stem diameters and heights, and a complex horizontal arrangement of stems (eg. Spies and Franklin 1991). It is therefore not surprising that the literature contains a number of studies in which measures of tree species richness and / or diversity have been used to characterise stand structure (eg. Sullivan *et al.* 2001, Maltamo 1997, Uuttera *et al.* 1997).

Species richness and diversity are particularly important attributes of tropical forests, and in some cases are more successful in distinguishing between primary and secondary forest than attributes such as mean diameter or number of trees (Uuttera *et al.* 2000, Ferreira *et al.* 1999). This contrasts with some temperate forests where it is the relative abundance of key tree species or groups of species, rather than species richness, which distinguishes successional stages. For example Ziegler (2000) found that old-growth hemlock-hardwood stands had a higher proportion of hemlock trees than regrowth stands. Similarly Spies and Franklin (1991) found that the density of shade intolerant tree species was the most significant explanatory variable in a multiple regression relating stand age to a range of structural attributes.

2.8 Understorey vegetation

Up to this point this review has focused on structural attributes associated with the trees in a stand, such as canopy layering, tree size variation, tree species richness, and the spatial arrangement of trees. This reflects a preoccupation in the international literature with characterising structure in terms of overstorey elements, with relatively little regard for the importance of other lifeforms. This may be partly justified on the grounds that overstorey structure influences the condition of the understorey. For example Berger and Puettmann (2000) found that in aspen-conifer forests herbaceous diversity was related to the basal area of the overstorey and to a measure of foliage height diversity, although shrub height and shrub cover were also important in explaining herbaceous diversity. A few notable studies have addressed the understorey directly and these are discussed below.

Spies and Franklin (1991) used 84 attributes to characterise the structure of unmanaged Douglas-fir forests. 14 of these attributes related directly to the understorey, and 6 of the 14 were significant in distinguishing between successional stages of Douglas-fir. In order of importance the understorey attributes were, % herbaceous layer cover, density of shade tolerant saplings, % cover of deciduous shrubs, density of subcanopy saplings, % total understorey cover, and coefficient of variation of herb cover.

Van Den Meersschaut and Vandekerkhove (1998) placed a similar emphasis on the understorey when developing a stand scale biodiversity index for forests in Belgium. In their index understorey attributes accounted for 25% of the total score, however unlike Spies and Franklin (1991) they placed relatively little importance on the amount of cover of the herb layer (3 out of 25). The highest weighting was given to the richness of understorey species (vascular species 10 out of 25, bryophytes 5 out of 25). Sullivan *et al.* (2001) also emphasised understorey species richness and diversity when characterising the structure of coniferous forests in the Pacific north-west. In their study herb and shrub species richness and diversity were treated as separate attributes of structure.

2.9 Dead wood

In contrast to understorey elements dead wood appears in the literature as a structural element comparable in importance to the overstorey trees. In their study of old-growth Douglas-fir forests Franklin *et al.* (1981: 41) concluded that, "To a large degree, success in managing forests for old-growth attributes will depend on learning to manage the dead organic matter (snags, logs and litter) as cleverly as the live trees." They attributed the distinctive features of old-growth Douglas-fir forests to four structural elements, three of which related to dead wood in the form of:

- large dead standing trees;
- large logs on land and;
- large logs in streams.

These elements have also been shown to play a key role in the provision of fauna habitat in old-growth Douglas-fir forests (Franklin *et al.* 1981).

Dead standing trees

The importance of dead standing trees (stags) as a structural attribute has been confirmed in subsequent studies in a variety of forest types (Bachofen and Zingg 2001, Svennson and Jeglum 2001, Sullivan *et al.* 2001, Van Den Meersschaut and Vandekerkhove 1998, Tyrell and Crow 1994, Spies and Franklin 1991). However there is little concensus amongst these studies as to how stags should be quantified. Franklin *et al.* (1981) quantified stags in old-growth Douglas-fir forests in terms of numbers per ha and mean dbh, and described but did not apply a system suggested by Cline (1980) for classifying stags into 5 decay classes. Franklin *et al.* (1981) considered decay classes to be an important attribute because different vertebrates utilised material from different classes.

In their study of unmanaged Douglas-fir forests Spies and Franklin (1991) used a more elaborate set of attributes to describe stags. This included number of stags per ha across two height classes and two diameter classes, stag volume across 5 decay classes, total stag volume, and the coefficient of variation (CV) of total stag volume. However one attribute, the number of stags 5 to 15m tall, explained most of the variation between successional stages that was attributable to standing dead wood.

Tyrrell and Crow (1994) also quantified stags in detail in order to characterise the structure of old-growth hemlock-hardwood forests. They described stags in terms of species, dbh, 4 height classes, 3 decay classes, basal area and total stag volume. The most useful of these was stag basal area which increased linearly with stand age.

Elaborate descriptions of stag condition may not therefore be particularly useful. A more practical approach may be to simply quantify stags in terms of their size and number. For example Van Den Meersschaut and Vandekerkhove (1998) assessed stags in terms of three simple attributes:

- Basal area of stags - to indicate the volume of dead wood;
- Number of large stags (dbh > 40cm) - to indicate the potential hollow bearing resource;
- Standard deviation of dbh - to indicate the variation in size of dead wood and associated hollows and hence its value to a diversity of fauna.

Logs

Dead standing trees are a primary source of logs and so to some extent measures which quantify stags may also be indicative of the potential log resource. Svennson and Jeglum (2001) acknowledged this relationship by describing dead wood in terms of 5 types based on whether or not a log existed which could be connected to a stag or stump.

However a number of studies that quantify dead wood have treated logs separately to stags. A wide variety of attributes have been used for this purpose including, total log volume, log volume or density by diameter or decay class, and the coefficients of variation in these attributes (eg. Tyrrell and Crow 1994, Spies and Franklin 1991). The most useful of these appear to be those attributes describing the abundance of large logs, and variation in log numbers and size. For example, of the 10 attributes used by Spies and Franklin (1991) to describe logs, only three (>60cm diameter log density, >60cm log density coefficient of variation and total log volume) were significant in a canonical discriminate analysis used to relate age classes of unmanaged Douglas-fir to a suite of structural variables. Similarly Van Den Meersshaut and Vandekerkhove (1998) described logs in their index of biodiversity in terms of the total length of large logs (>40cm) and the number of diameter classes present.

2.10 Conclusions

From the review presented above it is clear that a variety of approaches have been used to define structural attributes in the international literature. Different authors have emphasised subsets of different attributes, and very few studies have advocated similar suites of attributes. This lack of consensus may in part reflect differing rationales for selecting attributes in the first place. Some authors for example, chose attributes because they were useful for purposes other than characterising biodiversity, such as predicting the protective function of forests in avalanche prone areas (Bebi *et al.* 2001, Bachofen and Zingg 2001). Other authors chose attributes because they were relatively easy to measure and model, and were thought to be correlated with more complex attributes (eg. Wikstrom and Eriksson 2000, Gove 1996, Buongiorno *et al.* 1994). In some cases a limited suite of attributes was utilised because of historical precedent, such as systematic measurements carried out in permanent plots (Acker *et al.* 1998, Maltamo *et al.* 1997), or because attributes reflected the current state of a particular remote sensing technology (eg. Means *et al.* 1999).

In most cases attributes were assumed to be indicative of biodiversity, although few studies provided quantitative evidence linking attributes to the provision of wildlife habitat (Franklin *et al.* 1981 is a notable exception). A number of studies justified their selection of attributes on the grounds that these successfully distinguished between different successional stages (eg. Ziegler 2000, Tyrrell and Crow 1994, Spies and Franklin 1991). This seems a reasonable claim, since attributes which are changing or developing during succession are also likely to be those responsible for the different habitats associated with each successional stage.

While the international literature provides a guide as to which attributes are likely to be useful in characterising forest structure, it would be wrong to assume these attributes will be important or even relevant in characterising Australian ecosystems. To identify which attributes might best fit this role, the next section reviews Australian studies which have associated attributes of structure with the presence or abundance of fauna.

3. Stand level attributes – a review of Australian studies

3.1 Introduction

A total of 54 studies were identified in which the presence or abundance of different fauna were significantly associated with vegetation structural attributes in southeast or southwest Australia. Most of these associations involved direct correlations between attributes and the presence or abundance of fauna, although a few associations were in the form of significant effects in multivariate models. The scope of the studies varied considerably; some, such as Fauna Impact Statements, investigated a range of different faunal groups while others concentrated on a single faunal species. The relevant details for each study are summarised in Appendix 1. Table 2 indicates the proportion of studies which addressed seven broad faunal groups. The majority of work concerned bird, arboreal marsupial, and ground mammal habitat requirements, with relatively fewer studies addressing the habitat requirements of reptiles, invertebrates, bats or amphibians.

In addition to these 54 quantitative studies, a range of observational studies and reviews were also consulted. While these were not used to identify structural attributes they did provide additional information regarding the habitat requirements of the different faunal groups.

Table 2: The proportion of 54 studies which significantly associated vegetation structural attributes with the presence or abundance of species from different faunal groups. Some studies addressed species from more than one faunal group.

Arboreal marsupials	Birds	Ground mammals	Reptiles	Invertebrates	Bats	Amphibians
30%	26%	24%	15%	10%	8%	8%

For clarity the results of the review are presented in two stages. In the first stage the habitat requirements and associated structural attributes, which were identified by the review, are discussed for each faunal group (Sections 3.2 to 3.8). In the second stage, these attributes are combined to produce a core set of attributes, which characterises the habitat requirements of all faunal groups (Section 3.9).

3.2 Habitat resources used by birds

3.2.1 Introduction

The bird species occurring in eucalypt woodlands and forests belong to a variety of foraging groups, reflecting the diversity of resources which these vertebrates can utilise. A large proportion of birds are insectivorous, foraging for invertebrates in the leaves, branches and bark of eucalypts, in the air spaces provided by canopy gaps, and amongst litter and woody debris (Woinarski *et al.* 1997). There is also a diversity of bird species which feed on nectar and exudates such as manna, honeydew and sap (Recher *et al.* 1985). A small proportion of birds feed on eucalypt seeds, and only a very few species are capable of digesting pollen. Frugivorous birds are rare and there are no leaf eating birds (Landsberg and Cork 1997). In addition to food resources, birds utilise sites for nesting and shelter, either in the form of suitable tree hollows, or appropriate foliage or ground cover arrangements (Recher *et al.* 1991).

The most productive habitats for birds appear to be those providing a range of resources which can support a variety of different foraging groups (Bauer *et al.* 2000). This is most likely to occur where there is a diversity of vegetation strata available as foraging substrates (Gilmore 1985, Loyn 1985, Recher 1969, MacArthur and MacArthur 1961). In Australian temperate forests and woodlands different strata tend to reflect differences at the levels of plant life form (forb, shrub or tree) and plant genus. This provides different kinds of food (nectar, fruit, seeds) and foliage thereby increasing the diversity of foraging opportunities for bird species (Recher 1985).

Six habitat components have been consistently identified as important resource bases for birds (Recher *et al.* 1998, Woinarski *et al.* 1997, Traill 1993, Recher 1991, Gilmore 1985):

- Foliage; a source of exudates and invertebrates;
- Flowers; a source of nectar and invertebrates
- Bark; a source of exudates and invertebrates
- The ground layer, including ground vegetation, litter, logs and coarse woody debris; - a source of invertebrates and small vertebrates;
- Air spaces; within and between canopy strata - a source of invertebrates;
- Hollow bearing trees; for nesting and shelter.

A variety of structural attributes have been used to characterise these habitat components. These attributes and the literature relevant to each habitat component are discussed below. As a summary, those structural attributes which have been significantly associated with the presence, abundance or diversity of bird species or assemblages of species are listed in Table 3.

Table 3: Structural attributes positively associated with either the presence, abundance or richness of one or more bird species in eucalypt forests (F) or woodlands (W). (-) indicates a study reporting a negative association for some species.

Attribute	Study
Foliage Height Diversity (W)	Abbott 1976, Recher 1969
% cover canopy trees (F)(W)	Freudenberger 1999*, Smith *et al.* 1994, Andrews *et al.* 1994, Arnold *et al.* 1987(-), Gilmore 1985
Canopy height (F)(W)	Smith *et al.* 1994, Gilmore 1985
Canopy surface area and volume (F)(W)	Gilmore 1985
Number of overstorey stems (W)	Pearce 1996, Arnold *et al.* 1987
Basal area of overstorey stems (F)	Braithwaite *et al.* 1989
Overstorey species richness (F)	Bauer *et al.* 2000, Smith *et al.* 1994
Foliar nutrients (Magnesium index) (F)	Braithwaite *et al.* 1989
Flowering intensity index (F)	McGoldrick and MacNally 1998
Bark index (F)(W)	Pearce 1996, Gilmore 1985
% cover midstorey trees (F)	Fanning 1995,
Shrub species richness (W)	Seddon *et al.* 2001, Arnold *et al.* 1987,
% cover shrubs (F)(W)	Seddon *et al.* 2001, Freudenberger 1999*, Andrews *et al.*1994,
% cover herbs and grasses (F)(W)	Seddon *et al.* 2001, Freudenberger 1999*, Fanning 1995, Smith *et al.* 1994 (-), Andrews *et al.* 1994,
% cover or other measure of litter (F)(W)	Freudenberger 1999*, Smith *et al.* 1994, Gilmore 1985
% cover or other measure of log abundance (W)	Freudenberger 1999*, Laven *et al.* 1998
% cover bare soil (F)	Smith *et al.* 1994 (-)
Number of hollow bearing trees (F)	Seddon *et al.* 2001, Fanning 1995

*Attribute a component of Habitat Complexity Score, which was correlated with bird species richness

3.2.2 Bird habitat components

FOLIAGE

Foliage carbohydrate sources such as manna, lerp and honeydew form an important component of the diet of a wide range of bird species (Woinarski *et al.* 1997, Recher *et al.* 1985). These resources are more abundant on eucalypt rather than on non-eucalypt plant species, with lerp producing insects being most abundant on eucalypts with high foliar nutrient content (Recher *et al.* 1991). Attributes which are indirect measures of these carbohydrate resources are the basal area of eucalypts, and foliar magnesium, both of which have been correlated with bird species richness (Braithwaite *et al.* 1989).

The distribution and abundance of bird species have also been related to particular eucalypt subgenera. Loyn (1985) found that there were differences in the bird species associated with eucalypts from the *Symphyomyrtus* and *Monocalyptus* subgenera. This was attributed to differences in the invertebrates which occurred on the foliage of the two subgenera and to the relative abundance of hollow bearing trees in the *Symphyomyrtus* subgenus - although Gibbons (1999), found there were no significant differences between the subgenera in the rate of occupancy of hollows by fauna. Recher (1985) attributed an increased abundance and diversity of bird species in forests dominated by *Symphyomyrtus* to the typically higher foliage nutrient levels of this subgenus compared to the *Monocalyptus* subgenus.

Non-eucalypt species are also important to many foliage-gleaning insectivorous birds because these plants offer a greater diversity of foliage arrangements and associated invertebrates than eucalypts (Woinarski *et al.* 1997). Shrub cover and shrub species richness is a direct measure of this resource and has been repeatedly associated with bird species richness (Seddon *et al.* 2001, Andrews *et al.* 1994, Arnold *et al.* 1987, Recher *et al.* 1985).

Although there is relatively little foraging height specialisation amongst eucalypt and woodland birds (Recher *et al.* 1985), some bird assemblages have been shown to favour the foliage available in different vegetation strata. In a study of vegetation remnants in Western Australia, Arnold *et al.* (1987) found that Ravens, Magpies, Mudlarks and Galahs increased with greater tree canopy cover and less shrub cover, while the number of small insectivorous passerines increased as tree canopy decreased and shrub cover and shrub species increased.

The presence of different vegetation strata may also impact on the breeding success of birds. Most eucalypt forest birds nest within a specific layer of vegetation placing their nests among the foliage and small branches of trees and shrubs. The choice of nest site is often related to foliage density and plant species so that each bird species has a limited capacity to adjust its nesting height. Habitats with sparse foliage will usually support relatively few nest sites compared to habitats with a complex vegetation profile and dense foliage (Recher *et al.* 1991).

Gilmore (1985) found that canopy height was an effective and simple measure of the diversity of vegetation strata, and could be used to predict the density of insectivorous birds in woodlands and low forests.

FLOWERS – A TEMPORAL HABITAT COMPONENT

Birds are highly mobile and often depend on different habitats at different times of the year (Reid 1999). For example many nectarivorous birds follow the asynchronous flowering of eucalypt and understorey species, locating and exploiting sources of nectar production as they occur in different woodland and forest communities (McGoldrick and MacNally 1998, Traill 1993). To be able to do this, birds often nest in high quality sites from late winter to summer when abundant insect populations and foliage production provide the density of resources needed for reproduction. The birds are then free to either migrate, or to locate winter flowering eucalypts and shrubs elsewhere in the landscape (Loyn 1993, Recher 1985, Loyn 1985a).

The timing and abundance of these floral resources has been related to overstorey species composition (MacNally and McGoldrick 1997, Kavanagh 1984), the floristic diversity of the understorey (Pyke 1985, Recher 1985), and the presence of key species which flower profusely (Turner 1991), or at a critical time (Reid 1999, Loyn 1985a). Floral food resources have been also quantified using indices of flowering intensity, and these indices have been correlated with the abundance and richness of nectarivores (McGoldrick and MacNally 1998, Ford 1983).

Simple attributes such as shrub richness and cover, and the distribution of basal area amongst overstorey species may also effectively describe the potential floral resource. This is because these attributes indicate which plants are present and in what quantity.

BARK

Bark is an important habitat component in eucalypt forests and woodlands and is used to some degree by nearly all bird species. In some habitats bark can account for up to 25% of all foraging manoeuvres (Recher *et al.* 1985). Bark foraging birds utilise a range of invertebrates and sugar rich exudates found on and behind decorticating and non-decorticating bark (Recher *et al.* 1998, Loyn 1985). Decorticating bark may also provide perching sites which some birds require to access manna and to probe for arthropods (Pearce *et al.* 1994).

Noske (1985) indicated that variation in bark structure and bark type influences the distribution of bark-dwelling invertebrates and the foraging tactics of birds preying on them. A number of other studies also conclude that birds are likely to be locally diverse in association with the contrasting bark characteristics of mixed eucalypt communities (Woinarski *et al.* 1997, Landsberg and Cork 1997, Recher *et al.* 1991). Indices which quantify the availability of decorticating bark have been correlated with the presence of insectivorous birds (Pearce 1996, Gilmore 1985). However no studies appear to have quantified the importance of a diversity of bark types for bark foraging birds.

THE GROUND LAYER

Ground foraging birds, which utilise ground vegetation (grass, herbs), litter, logs and coarse woody debris as foraging substrates are one of the most abundant bird communities in woodlands and forests in south-western and south-eastern Australia (Recher *et al.* 1998). This reflects the absence of dense ground vegetation in many woodlands and dry sclerophyll forests, and the accumulation of litter and woody debris in wet and dry sclerophyll forests (Bauer *et al.* 2000, Recher *et al.* 1998, Woinarski *et al.* 1997). Many threatened and declining bird species in western NSW are ground foraging insectivorous birds and this has been partly attributed to the loss of a structurally diverse ground layer with abundant litter and coarse woody debris (Reid 1999).

Litter and woody debris are relatively straightforward to quantify, and both have been used to characterise the value of the ground layer for birds. Smith *et al.* (1994) described the litter layer in terms of percentage litter cover, and showed that this was positively correlated with the richness of ground foraging bird species and negatively correlated with the cover of grasses and herbs. However litter cover only partially describes the resource available for ground foragers because the depth of the litter layer will vary within and between habitats. If litter fall is assumed to be in equilibrium with litter decomposition, then the dry mass of litter is a better measure of available organic matter and this has been correlated with the density of ground foraging birds (Gilmore 1985).

Relatively few studies have quantified the role of fallen timber in bird microhabitat, although it appears likely that woody debris will provide significant food and foraging opportunities, and shelter sites (Reid 1999, Recher *et al.* 1998). Laven and MacNally (1998) found that piles of fallen timber influenced the spatial location of birds in Victorian Box-Ironbark forests. Bird numbers were nine times greater and bird species three times richer in areas containing piles of woody debris.

CANOPY AIR SPACES

The air spaces within and between canopy layers are an important source of invertebrates for insectivorous birds (Landsberg and Cork 1997, Recher 1991). In one of the few studies which have attempted to quantify this resource Gilmore (1985) correlated the density of aerial foraging insectivores with an index of tree crown surface area. This index required measurements of individual tree crowns, and Gilmore concluded that canopy height was the simplest estimator of insectivore densities.

HOLLOWS

Of the 531 bird species in Australia, 18% (94 species) utilise hollows, and 11% (57 species) are obligate hollow users (Saunders *et al.* 1982). For many of these species the availability of hollows can determine their presence or absence from a given site (MacNally *et al.* 2000, Traill 1991). Several authors have found a significant relationship between the density of tree hollows and the diversity of forest or woodland bird species (Seddon *et al.* 2001, Fanning 1995). However this relationship has not been replicated for some hollow-dependent species such as owls, parrots, rosellas, and cockatoos. These species can travel long distances and consequently the number of hollows measured at a particular site may not reflect the availability of hollows over a larger area (Smith *et al.* 1994, Andrews *et al.* 1994).

Choice of nest hollow characteristics can be highly specific with different bird species preferring smooth rather than rough openings to the hollow, or dead rather than living trees, or one tree species over another (Recher 1991). Competition for hollows can occur between bird species which utilise the same type of hollow, and in this situation dominant species may exclude other species by occupying all suitable hollows (Newton 1994). A diversity of hollow types rather than an abundance of a few types, is therefore more likely to support a diversity of bird species.

3.3 Habitat resources used by arboreal marsupials

3.3.1 Introduction

Arboreal marsupials comprise approximately 20% of the 400 species of vertebrates which utilise tree hollows in Australian forests and woodlands (Gibbons *et al.* 1997, Gibbons and Lindenmayer 1996). Their distribution and abundance in the landscape is often patchy (Braithwaite *et al.* 1983), reflecting an association with high quality and floristically diverse areas of forest (Pausas *et al.* 1994, Davey 1984). These areas are preferred because they are likely to provide year round resources at a scale comparable with the home ranges of arboreal marsupials (Eyre and Smith 1997, MacFarlane 1988, Kavanagh 1984,1987). Trees that flower or shed their bark in winter are particularly important, and where these are missing animals are also absent or only present in low numbers (Soderquist and MacNally 2000, Kavanagh 1987).

The following four habitat components appear to provide critical resources for arboreal marsupials (Lindenmayer *et al.* 1999c, Eyre and Smith 1997, Cork and Catling 1996, Pausas *et al.* 1995, Lindenmayer *et al.* 1990a, Kavanagh 1984)

- Foliage; a source of edible leaf material;
- Flowers; a source of nectar and pollen;
- Bark; a source of exudates and invertebrates;
- Hollows; as den and nesting sites.

A variety of structural attributes have been used to characterise these habitat components and those attributes which have been significantly associated with the presence, abundance or richness of arboreal marsupials are listed in Table 4.

Table 4: Structural attributes positively associated with either the presence, abundance or richness of one or more arboreal marsupial species in eucalypt forests (F) or woodlands (W).

Attribute	**Study**
Basal area of overstorey stems (F)(W)	Munks *et al.* 1996, Braithwaite *et al.* 1983,
Number or basal area of large trees (>60cm^{A},>80cm^{B}, other^{C}) used directly or as part of an index (F)	Soderquist *et al.* 2000^{BC}. Pausas *et al.* 1995^{A}, Andrews *et al.* 1994^{B}, Kavanagh *et al.* 1990^{B}, Hindell *et al.* 1987^{C}, Braithwaite *et al.* 1983^{AB}
Overstorey diversity (Shannon Weaver Index^{D}, species richness^{E}) (F)(W)	Braithwaite *et al.* 1983^{D}, Munks *et al.* 1996^{E}
Overstorey species composition (F) (used directly or as part of an index)	SFNSW 2000, Eyre *et al.* 1997, Pausas *et al.* 1995, Kavanagh 1990, Hindel *et al.* 1987
Canopy height (Site height^{F}) (F)	Soderquist *et al.* 2000, Eyre *et al.* 1997^{F}, Smith *et al.* 1994
Foliage density at different heights or strata (F)	Jackson 2000, Davey 1984
Number of hollows (visible or predicted) (F)	Gibbons *et al.* 2002, Soderquist *et al.* 2000, Pausas *et al.* 1995, Lindenmayer *et al.* 1990a,
Number of hollow bearing trees (F)	Smith *et al.* 1994, Lindenmayer *et al.* 1991a, Lindenmayer *et al.* 1990b,
Spatial distribution of hollow bearing trees (F)	Lindenmayer *et al.* 1990a,
Measures of foliar nutrients (including leaf water content) (F)(W)	Munks *et al.* 1996, Pausas *et al.* 1995, Kavanagh *et al.* 1990, Braithwaite *et al.* 1983,
Eucalypt species richness (F)	Bauer *et al.* 2000,
% cover canopy trees (F)	Andrews *et al.* 1994,
% cover shrubs or other abundance measure (F)	Andrews *et al.* 1994, Lindenmayer *et al.* 1990b, Lindenmayer *et al.* 1991a,
Flowering Index (F)	Kavanagh 1987
Bark index (F)	Pausas *et al.* 1995, Lindenmayer *et al.* 1990a, Kavanagh 1987,
Basal area (abundance^{G}) of acacia species (F)(W)	Jackson 2000^{G}, Munks *et al.* 1996, Lindenmayer *et al.* 1990a, Lindenmayer *et al.* 1990b,

3.3.2 Arboreal marsupial habitat components

FOLIAGE

Many studies have demonstrated the importance of foliar nutrient concentration in controlling the distribution and abundance of arboreal marsupials in eucalypt forests and woodlands (Munks *et al.* 1996, Pausas *et al.* 1995, Kavanagh *et al.* 1990, Braithwaite *et al.* 1983). At a micro-scale animals appear to preferentially browse on young leaves of particular tree species so as to maximise their intake of foliar nitrogen and minimise the bulk of indigestible fibre (Kavanagh *et al.* 1990). At a macro-scale animals are associated with high quality sites that are floristically diverse, because this increases the choice of food sources, so that at any one time the most nutritious foliage can be selected (Pausas *et al.* 1994, Braithwaite *et al.* 1983).

In light of these preferences a critical threshold in foliage nutrients for arboreal folivores has been suggested, with forests whose leaves fall below this threshold unable to sustain populations of arboreal marsupials (Cork and Catling 1996, Pausas *et al.* 1995). Such a threshold may explain the concentration of 63% of arboreal marsupials in only 9% of the forest area of southeast NSW (Cork and Catling 1996, Braithwaite *et al.* 1983).

In addition to the quality of foliage, its vertical arrangement also affects the abundance and diversity of arboreal folivores. Different species have been shown to utilise different strata within the canopy and to prefer different densities of foliage (Jackson 2000, Smith *et al.* 1994, MacFarlane 1988, Davey 1984). Vertical complexity is likely to be associated with high levels of floristic diversity, since this provides a range of plants with different foliage densities, height development and shade tolerance (Florence 1996, Davey 1984)

Simple attributes, which have been used to quantify the foliage component of arboreal habitat, include stand basal area, canopy height and overstorey species composition. Stand basal area and canopy height are simple measures of site fertility, canopy biomass and vertical complexity (Carron 1968 cited in Davey 1984), and both have been correlated with the abundance of arboreal marsupials (Eyre and Smith 1997, Smith *et al.* 1994, Braithwaite 1983).. Overstorey species richness is a direct measure of floristic diversity and has also been correlated with the abundance and diversity of arboreal mammals (Bauer *et al.* 2000, Braithwaite *et al.* 1983).

FLOWERING

The distribution and abundance of flowering plants, particularly those flowering in winter, has been shown to be critical for a range of arboreal species (Soderquist and MacNally 2000, Smith *et al.* 1994, Andrews *et al.* 1994, Kavanagh 1987). Although indices have been developed to quantify the resources provided by flowers (Kavanagh 1987), in practice these can be complex to use. Quantifying the temporal availability of flowering resources is also difficult because it requires multiple measurements over successive time periods. Since the timing and abundance of flowering depends largely on the species present and the size of the trees (Smith *et al.* 1994, Kavanagh 1987), attributes such as, distribution of basal area amongst overstorey species, and mean dbh, may provide a simple and more practical means of characterising the availability of floral resources.

BARK

Bark is an important resource for arboreal marsupials because many species forage for invertebrates which shelter under decorticating bark (Eyre and Smith 1997, Lindenmayer *et al.* 1990a). These invertebrates provide an important source of protein in the diet of many arboreal marsupials. Large numbers of invertebrates over-winter under the bark of eucalypts, so that tree species which shed their bark in winter increase the availability of this food resource at a critical time of the year (Kavanagh 1984). Large gum barked trees may be particularly important because their large surface area of decorticating bark provides a concentrated source of invertebrates and exudates (Eyre and Smith 1997). The presence and abundance of a range of arboreal species have been correlated with indices which quantify the amount of decorticating bark (Pausas *et al.* 1995, Lindenmayer *et al.* 1990a, Kavanagh 1987). Simpler attributes also likely to characterise bark resources are the distribution of basal area amongst overstorey species, and mean dbh.

In addition to invertebrates, sap exudates present on the bark of acacia understorey species provide important carbohydrate sources for arboreal marsupials. The basal area of acacia species is an indirect measure of this resource and has been correlated with the abundance and diversity of arboreal marsupials in the Mountain Ash forests of Victoria (Lindenmayer *et al.* 1991a).

HOLLOWS

The presence, abundance and diversity of arboreal marsupials has been consistently correlated with the number of hollow bearing trees (Lindenmayer and Franklin 1997, Gibbons and Lindenmayer 1996, Smith *et al.* 1994). Low numbers of hollow bearing trees have also been shown to limit densities of arboreal marsupials in both forests and woodlands (Bauer *et al.* 2000, Lindenmayer *et al.* 1999c, Lindenmayer *et al.* 1991a, Traill 1991, Lindenmayer *et al.* 1990b).

Dbh is the most common attribute used to describe the availability and occupancy of hollow bearing trees for fauna (Gibbons *et al.* 2000, Shelley 1998, Pausas *et al.* 1995, Bennet *et al.* 1994, Lindenmayer *et al.* 1991b, MacKowski 1984). High basal area, which often reflects a mature stand, may also be indicative of the presence of hollow bearing trees (Braithwaite *et al.* 1983). In a review of 13 different studies which addressed the occupancy of trees by hollow dependent fauna, Gibbons *et al.* (2002), found that 80% of studies reported a significant correlation between occupancy and tree dbh. As an attribute dbh should include dead as well as live trees, because dead trees may account for up to 18.5% of all trees with hollows, and are preferred by some arboreal vertebrate species (Gibbons *et al.* 2002).

While trees with larger dbh are likely to contain more occupied hollows, Gibbons *et al.* (2002) found that these were predominantly large hollows, with relatively few small occupied hollows. Different arboreal species utilise different sized hollows, both in terms of preferred entry size and internal hollow dimensions (Whitford 2001, Lindenmayer and Franklin 1997, Gibbons and Lindenmayer 1996), so that maximum diversity of arboreal fauna will require a range of hollow bearing tree sizes. Overstorey species composition may also be an attribute associated with a diversity of hollow types, because eucalypt species can develop different types of cavity as a result of differences in growth form and morphology, and in their susceptibility to attack by decay organisms (Lindenmayer *et al.* 2000b). On this basis, the potential hollow resource for arboreal species is better described by the average dbh of living and dead trees, its coefficient of variation, and overstorey species composition, rather than by tree dbh alone.

In addition to these attributes, the spatial distribution of hollow bearing trees is an important consideration. Lindenmayer *et al.* (1990a) found that the territorial behaviour of some arboreal species limited the availability of hollows when trees were clustered rather than more uniformly spaced. The spacing of hollow bearing trees has been quantified using the Cox Index of clumping, which is the variance to mean ratio of the number of hollow bearing trees per unit area (Lindenmayer *et al.* 1990a, Cox 1971 cited in Neumann and Starlinger 2001).

3.4 Habitat resources used by ground dwelling mammals

3.4.1 Introduction

Habitat quality for ground dwelling mammals appears to be primarily determined by understorey complexity (Cork and Catling 1996). Four habitat components have been commonly used to characterise the understorey resources which are important to ground mammals:

1) Shrub cover; for shelter and refuge from predators;
2) Logs and coarse woody debris; for shelter and nesting and as a source of invertebrates and edible fungi;
3) Litter; for nesting and as a source of invertebrates;
4) Rocks; for refuge and den sites.

A variety of structural attributes have been used to quantify these habitat components and those attributes which have been significantly associated with the presence, abundance or richness of one or more species of ground mammal are listed in Table 5.

Different groups of ground mammal species are often associated with different levels of complexity in the arrangement of the four structural components listed above (Cork and Catling 1996, Catling *et al.* 1995, Barnet *et al.* 1978). Large mammals such as the eastern grey kangaroo and the common wombat prefer an open understorey with scattered shrubs and a ground cover of grasses and are likely to increase in abundance as understorey complexity decreases (Catling and Burt 1995); whereas small to medium sized ground mammals such as antechinus, potoroos and bandicoots prefer a complex understorey having a diverse shrub layer and a ground cover of logs, leaf litter and woody debris (Paull and Date 1999). Some ground mammals require mosaics or ecotones that allow the inclusion of contrasting microhabitats within their home ranges (Smith *et al.* 1994). Long-nosed potoroos for example utilise a range of vegetation densities – thick cover for shelter and protection from predators and open areas to forage for hypogeal fungi (Claridge and Barry 2000, Bennett 1993).

The utilisation of a range of vegetation structures by ground mammals implies that maximum diversity of ground mammals is likely to occur in habitats comprising a small scale mosaic of dense and open vegetation patches (Lunney and Ashby 1987). This type of heterogeneity could be quantified by coefficients of variation in structural attributes such as basal area of overstorey species, tree dbh, and percentage cover of overstorey and understorey species.

However to date such measures have not been used to characterise the habitat of ground mammals (Claridge and Barry 2000).

Table 5: Structural attributes positively associated with either the presence, abundance or richness of one or more ground dwelling mammal species in eucalypt forests (F). (-) indicates a study reporting a negative association for some species. There were no relevant studies for woodlands.

Attribute	**Study**
Basal area of overstorey stems (F)	Catling *et al.* 2000, Catling *et al.* 1998, Catling *et al.* 1995
% canopy cover (F)	Andrews *et al.* 1994
Shrub and overstorey species richness (F)	Bennett 1993
% midstorey cover (F)	Andrews *et al.* 1994
% cover of shrubs (tall and/or low) (F)	Bauer *et al.* 2000, Claridge *et al.* 2000, Catling *et al.* 2000(-), Lunney *et al.* 1988, Arnold *et al.* 1987, Barnett *et al.* 1978
Vertical density of shrub layer foliage (F)	Bennett 1993
Measures of abundance of large logs (F)	Bauer *et al.* 2000, Andrews *et al.* 1994, Smith *et al.* 1994, Bennett 1993, Smith *et al.* 1989, Barnett *et al.* 1978
% cover of debris (litter, logs and rocks) (F)	Catling *et al.* 2000, Catling *et al.* 1998
% cover of litter (F)	Andrews *et al.* 1994, Barnett *et al.* 1978
Index of structural complexity (F)	Catling *et al.* 2000(-), Catling *et al.* 1995(-), Barnett *et al.* 1978

3.4.2 Ground dwelling mammal habitat components

SHRUB COVER

Understorey vegetation provides shelter and cover for a wide range of ground mammals. Medium to large ground mammals such as the eastern grey kangaroo and common wombat utilise patches of dense vegetation to provide cover adjacent to open habitats with a grassy understorey for grazing (Catling *et al.* 2000, Lunney and O'Connell 1988). Small ground mammals such as the brown antechinus, yellow-footed antechinus and fawn footed melomys have a preference for densely vegetated habitats with a well developed shrub layer in which they can hide and forage for invertebrates (Catling *et al.* 2000, Catling and Burt 1995, Smith *et al.* 1994, Bennett 1993).

Attributes such as percentage cover of shrubs, the vertical density of shrub foliage, and the floristic richness of the shrub layer have been used to quantify shrub cover, and each has been associated with the presence or abundance of a range of small, medium or large ground mammals (Catling *et al.* 2000, Claridge and Barry 2000, Catling and Burt 1995, Smith *et al.* 1994, Bennett 1993). The abundance of medium and large mammals has also been correlated with the basal area of overstorey species. This reflects a decline in shrub cover associated with an increasing basal area of the overstorey (Catling *et al.* 2000, Catling *et al.* 1998, Catling and Burt 1995)

LOGS AND WOODY DEBRIS

Logs are a critical resource for small ground mammals. They provide shelter from weather, refuge from predators (Woinarski *et al.* 1997), nesting sites for lactating females (Woodgate *et al.* 1994, Smith *et al.* 1989), and in seasonally cold climates logs reduce energy expenditure for hibernating species such as the echidna (Smith *et al.* 1989). Logs are also important for the mobility of small ground mammals, providing easily traversed travel routes through dense undergrowth (Halstead-Smith cited in MacNally *et al.* 2001, Woodgate *et al.* 1994). A variety of log sizes and conditions are utilised by small ground mammals, ranging from dry intact hollow logs for nest sites (Smith *et al.* 1989), to decomposing moist logs which provide a substrate for food resources such as hypogeal fungi and invertebrates (Woodgate *et al.* 1994, Dickman 1991). Mature hollow bearing trees are indirectly a critical resource for many small ground mammals because these trees are the future source of hollow logs (Smith *et al.* 1994, Andrews *et al.* 1994, Dickman 1991)

The richness of small ground dwelling mammal species has been correlated with the abundance of large logs (Bauer *et al.* 2000, Smith *et al.* 1994, Andrews *et al.* 1994) as has been the density of individual species such as the yellow footed antechinus (MacNally *et al.* 2001). However Bowman *et al.* (2000), found no relationship between abundance of logs or log decay class and small ground mammals, and attributed this to the fact that coarse woody debris was not a limiting factor in any of their study sites.

LITTER

Some small ground mammals utilise a deep litter layer in which to burrow for shelter and to forage for invertebrates (Dickman 1991, MacFarlane 1988). Percentage cover of litter is the attribute commonly used to quantify this resource, and has been correlated with the abundance of a number of small ground mammals including *Antechinus stuartii* and *Melomys cervinipes* (Barnett *et al.* 1978)

ROCKS

Rocky areas can provide shelter and refuge sites for a range of ground mammals including echidna, wallaroo, brush-tailed wallaby, rock wallaby, and tiger quoll (Paull and Date 1999). However no studies appear to have quantified the value of this resource, or to have correlated it with the presence or abundance of ground mammals. Newsome and Catling (1979) incorporated rock cover into a measure of litter cover, which also included logs, woody debris and leaf litter. This measure formed part of an index of habitat complexity, which was correlated with the presence and abundance of ground dwelling mammals (Catling *et al.* 2000, Catling and Burt 1995).

3.5 Habitat resources used by bats

3.5.1 Introduction

Bats comprise more than 25% of mammal species in Australia (Smith *et al.* 1994). Their diversity is largely determined by foliage structure, with many bat species exhibiting distinct foraging preferences for particular vegetation layers (Brown *et al.* 1997, Andrews *et al.* 1994, O'Neill and Taylor 1986) Species with large wing areas and small mass are slow flying yet highly manoeuvrable and prefer to forage in dense forest layers, whereas large fast flying species are less manoeuvrable and prefer open spaces above forests or within mid-storey gaps below tree crowns (Brown *et al.* 1997, Andrews *et al.* 1994). The richest bat assemblages tend to occur on high productivity sites with well developed vegetation strata (Smith *et al.* 1994).

Three habitat components appear to determine the presence and abundance of bat species:

1) Foliage and canopy spaces: for foraging;
2) Hollows and decorticating bark: for roost and nesting sites;
3) Permanent water;

The structural attributes which have been used to quantify these habitat components are listed in Table 6. The individual habitat components are then discussed below.

Table 6: Structural attributes positively associated with either the presence, abundance or richness of one or more species of bats in eucalypt forests (F) or woodlands (W). (-) indicates a study which reported a negative association.

Attribute	**Study**
Overstorey dbh (F)	Lunney *et al.* 1988
Canopy height (F)	Brown *et al.* 1997
Diameter distribution amongst overstorey species(F)	Lunney *et al.* 1988
Height difference between canopy and midstorey (F)	Brown *et al.* 1997
Midstorey height (F)	Brown *et al.* 1997
% cover of midstorey (F)	Andrews *et al.* 1994 (-)
% cover of shrubs (F)	Smith *et al.* 1994
% cover of litter (F)	Andrews *et al.* 1994 (-)
% cover of grass (F)	Andrews *et al.* 1994
Maximum dbh unburnt trees (F)	Andrews *et al.* 1994

3.5.2 Bat habitat components

FOLIAGE AND CANOPY SPACES

Insectivorous bats forage on and amongst plant foliage, and in the air spaces between different vegetation layers. O'Neill and Taylor (1986) identified four distinct foraging patterns in Tasmanian bat species:

- Slow highly manoeuvrable species, which foraged close to ground vegetation and the shrub layer;
- Faster manoeuvrable species, which foraged in and above the shrub layer;
- Fast but less agile species, which foraged in the space between the top of the understorey and canopy;
- Fastest but least agile species, which foraged above or just below the overstorey.

O'Neill and Taylor (1986) concluded that maximum diversity of bat species would require a patchy canopy with well developed shrub and subcanopy strata.

Brown *et al.* (1997) found that insectivorous bat activity increased with stand age in montane ash forests in central Victoria, reflecting increased vertical separation between the primary and secondary strata. The space between these two strata also became less cluttered as the number of overstorey stems declined. Bat activity was significantly correlated with the height of the primary tree stratum, the height of the secondary tree stratum and the height difference between these two strata.

HOLLOW BEARING TREES

Hollow bearing trees are utilised by bats for roosting, hibernation and maternity sites (Brown *et al.* 1997), and more than half of the 50 species of microchiropteran bats which occur in Australia are known to be hollow dependent (Tidemann and Flavel 1987). Bats can occupy small hollows when roosting singly, but may require large hollows for communal roosts, in which more than 200 individuals can occupy a single large tree (Tidemann and Flavel 1987). Lunney *et al.* (1988) found that *Nyctophilus gouldii* roosted only in trees with a dbh greater than 80cm and that roost sites were changed daily, so that multiple hollow bearing trees were required for each individual or colony. Taylor and Savva (1988) found that trees with a dbh greater than 120cm were preferred as roost sites.

Despite the importance of large hollow bearing trees to many bat species, stand level attributes such as the number of hollow bearing trees or tree dbh will not necessarily be correlated with the presence or abundance of bats. This is because bats have large home ranges and may travel two or more kilometres from roost to foraging site (Brown *et al.* 1997, Smith *et al.* 1994). The mobility and communal organisation of many bat species also means that unlike arboreal marsupials, bats will tolerate the clustering of hollow bearing trees used for roosting (Smith *et al.* 1994). The abundance of hollow dependent bats has been positively correlated with the maximum dbh of unburnt trees (Andrews *et al.* 1994), although this attribute was more directly a measure of understorey complexity than hollow development.

In addition to hollows within trees, bats may also roost in crevices under peeling bark. Dead trees are an important source of this type of roost site, forming a series of crevices as the bark separates from the main stem. These crevices are preferred roosting sites for a number of bat species (Taylor and Savva 1988, Lunney et al 1988). Lunney *et al.* (1988) also found that the distribution of size classes amongst overstorey species was a significant factor controlling roost selection. In their study, Gould’s long-eared bat preferentially roosted in large trees of particular overstorey species, a choice which in part reflected the production of decorticating bark, and in part the development of hollows.

WATER

Easy access to water is important for bats. Species which hibernate in cool, high elevation forests need to arise periodically in winter because body water turnover is higher than energy turnover. Water sources close to hibernating sites ensure that stored fat is not wasted in long flights (Smith *et al.* 1994). Similarly in semi-arid zones most bat species are restricted to moist environments associated with rivers, lakes and dams (Lumsden and Bennett 1995). Although roost sites have been shown to be associated with proximity to water (Tidemann and Flavel 1987) no study has correlated bat abundance or richness with distance to permanent water source.

3.6 Habitat resources used by reptiles

3.6.1 Introduction

In contrast to the detailed documentation of the habitat requirements of birds and mammals in southeast Australia relatively fewer studies have related reptile abundance and richness to particular habitat components (Woinarski *et al.* 1997, Brown and Nelson 1993). From available literature the following habitat components have been associated with reptile abundance:

1) <u>Insolation;</u> for body temperature regulation
2) <u>Logs and woody debris;</u> for shelter, basking and foraging for prey;
3) <u>Standing dead trees;</u> for shelter and foraging;
4) <u>Litter;</u> for foraging and cover;
5) <u>Shrubs;</u> for cover, invertebrate prey, and foliage input to the litter layer;

The structural attributes which have been used to quantify these habitat components are listed in Table 7. The individual habitat components are then discussed below.

Table 7: Structural attributes positively associated with either the presence, abundance or richness of one or more species of reptiles in eucalypt forests (F) or woodlands (W). (-) indicates a study which reported a negative association.

Attribute	Study
Abundance of large dead trees (F)	Andrews *et al.* 1994
Mean dbh of dead trees (F)	Brown and Nelson 1993 (-)
% cover or other measure of shrub abundance (F)(W)	Brown 2001, Bauer *et al.* 2000, Hadden *et al.* 1996, Arnold *et al.* 1987
Shrub species richness (F)(W)	Brown 2001, Hadden *et al.* 1996
% cover or other measure of log abundance (F)	Bauer *et al.* 2000, Andrews *et al.* 1994, Brown and Nelson 1993(-)
Measure of litter abundance (%cover, depth) (F)	Brown 2001, Smith *et al.* 1996, Brown and Nelson 1993 (-)
% cover of grass (F)	Brown 2001, Brown and Nelson 1993 (-)
Presence of a lichen crust (W)	Smith *et al.* 1996
% cover of bare ground (F)	Brown and Nelson 1993 (-)
% rock cover (F)	Fanning 1995

3.6.2 Reptile habitat components

INSOLATION

The availability of insolation appears to be the most important determinant of reptile habitat because reptiles depend on external heat sources to regulate their body temperature (Bauer *et al.* 2000, Andrews *et al.* 1994, Brown and Nelson 1993). To absorb heat many reptile species utilise rock outcrops for sun-basking sites, and Fanning (1995) found that reptile species richness was significantly higher at sites containing these ground features. Lunney *et al.* (1991) demonstrated the role of canopy structure in regulating insolation. They found that the uniformity of tree size and shape in regrowth forests in southeast NSW reduced the amount of sunlight reaching the ground. The rarity of normally common lizard species in these regrowth forests was attributed to a shortage of basking sites.

Brown and Nelson (1993) found that the insolation requirements of reptile species can differ significantly, indicating that a diversity of reptiles will require a range of lighting conditions from direct to semi-shaded (Woinarski *et al.* 1997). These conditions are most likely to be provided by a patchy canopy (Lunney *et al.* 1991). Patchiness can be quantified by attributes such as the coefficient of variation of canopy cover or coefficient of variation of tree dbh. To date no studies have attempted to correlate these attributes with reptile abundance or richness.

LOGS AND WOODY DEBRIS

Logs and woody debris provide foraging, basking, nesting and hibernation sites for reptiles (Lindenmayer and Franklin 1997, Brown and Nelson 1993, Slip and Shine 1988, Web 1985). Large logs which hold moisture can also act as refuges for reptiles during drought and fire (Andrews *et al.* 1994). Reptile abundance and richness have been significantly correlated with attributes which quantify log abundance such as percentage cover of logs, log length and number of logs (Bauer *et al.* 2000, Andrews *et al.* 1994). However in the Mountain Ash forests of the Victorian Highlands, Brown and Nelson (1993) found a negative relationship between the number of logs and reptile abundance. They attributed this to large numbers of logs being indicative of older forests, which provide little insolation for reptiles.

STANDING DEAD TREES

Hollows, and crevasses in the wood and bark of standing dead trees can provide important shelter and foraging sites for arboreal reptile fauna (Bauer *et* *al.* 2000). Reptile richness has been correlated with the numbers of dead trees (Andrews *et al.* 1994), although in Mountain Ash forest, Brown and Nelson (1993) found reptile abundance to be negatively correlated with the mean diameter of dead trees.

LITTER

Litter provides ground foraging reptiles with invertebrates for food, and a range of sites for shelter and basking. Decorticating bark is an important component of litter for ground dwelling reptiles. Brown and Nelson (1993) observed that lizards preferentially foraged in bark compared to other litter components. However no studies have attempted to relate the abundance of reptiles with measures of decorticating bark. Larger predatory reptiles such as varanids are indirectly dependent on the litter layer because they require a source of ground reptiles for prey (Recher and Lin 1990).

Attributes which measure the quantity of litter such as percentage cover and litter depth have been significantly correlated with reptile abundance (Brown 2001, Smith *et al.* 1996, Brown and Nelson 1993).

SHRUBS

Reptiles can be significantly more abundant in forests with well developed shrub and ground vegetation layers (Brown 2001). Shrubs provide invertebrate prey for reptile species (Woinarski *et al.* 1997), and contribute plant material to the litter layer. A dense shrubby understorey produces a thick moist litter layer important for some litter dwelling skinks (Woinarski *et al.* 1997); whereas a simplified shrub layer produces a sparse litter layer, and in Cypress Pine forests this has been shown to reduce reptile abundance and richness (Bauer *et al.* 2000). However in Mountain Ash forests a sparse litter layer can be indicative of reduced canopy and / or shrub cover, which can increase insolation at ground level. In these wet environments the abundance of some heliothermic reptiles has been negatively correlated with litter depth (Brown and Nelson 1993).

Attributes such as shrub richness, percentage cover of shrubs, and numbers of shrub stems have been used to quantify shrub resources for reptiles (Brown 2001, Bauer *et al.* 2000, Hadden *et al.* 1996, Arnold *et al.* 1987)

3.7 Habitat resources used by amphibians

3.7.1 Amphibian habitat components

The ecological requirements of Australian amphibians are poorly documented compared to other faunal groups (Hazell et al 2000, Lemckert and Brassil 2000). Despite this situation three habitat components have been identified as important for the survival of amphibians:
1) Proximity to free water; to maintain body moisture and for reproduction;
2) Vegetation cover; to maintain a moist micro-environment and for shelter;
3) Ground debris; for shelter and refuge sites.

Of these three habitat components water is the most important (Bauer *et al.* 2000, Parris and McCarthy 1999, Fanning 1995, Smith *et al.* 1994). This is because amphibians need to maintain a moist skin, and usually require free water for reproduction and the subsequent development of their young (Smith *et al.* 1994); although some species can breed in moist litter or boggy seepages (Andrews *et al.* 1994).

Overstorey canopy cover and understorey vegetation are important to amphibians through their role in maintaining a moist micro-environment. These features provide cover, which ameliorates the light, temperature, moisture and humidity conditions at ground level (Ferrai and Burgin 1993). Understorey vegetation and ground debris such as logs, rocks and litter also provide shelter and refuge from predation (Ferraro and Burgin 1993). The presence of these features at the aquatic terrestrial boundary can be critical during metamorphosis when mobility is limited by the process of tail resorption. Hazell *et al.* (2000) found that frog species richness was significantly higher when grass tussocks were present in the riparian zone, and was negatively correlated with the % cover of bare ground. Similarly, Bauer *et al.* (2000) attributed the scarcity of amphibians in the Cypress Pine forests of south-west NSW to a lack of aquatic resources and of suitable cover adjacent to the few water bodies that were present.

Relatively few studies have correlated the presence or abundance of amphibian species with vegetation structural attributes. This may in part reflect the scarcity of amphibians in many forest and woodland systems, but also the reliance of surveys on opportunistic sightings, which limits any statistical analysis of habitat associations (Andrews *et al.* 1994, Smith *et al.* 1994).

Those structural attributes which have been used to quantify amphibian habitat components are listed in Table 8.

Table 8: Structural attributes positively associated with either the abundance or richness of species of amphibians in eucalypt forests (F), and woodlands (W). (-) indicates a study which reported a negative association.

Attribute	**Study**
% cover of litter (F)	Smith *et al.* 1994
Presence of tussocks in the riparian zone (F)(W)	Hazell et al 2000
Stream size (F)	Parris and McCarthy 1999
% cover of bare ground in riparian zone (F)(W)	Hazell et al 2000 (-)
% of water body containing emergent vegetation (F)(W)	Hazell et al 2000
Log cover (classes) (F)	Andrews *et al.* 1994

3.8 Habitat resources used by invertebrates

3.8.1 Introduction

Eucalypt forests and woodlands provide three broad habitats for invertebrates - overstorey trees, understorey shrubs and grasses, and the ground layer of litter, woody debris and bare earth (Majer *et al.* 1997). Within these habitats the spatial scale at which invertebrate diversity occurs can be small, and individual plants or forest patches may support distinct invertebrate communities reflecting differences in bark, foliage and litter characteristics (Doherty *et al.* 2000, Majer *et al.* 1997, Recher *et al.* 1996). At the single tree scale, the richness of invertebrate species is determined by the structural complexity of the plant, its biochemical defences against attack and its foliage nutrient levels (Majer *et al.* 1997). The richest invertebrate communities have been associated with large old eucalypts because these are structurally more complex than younger trees (Recher *et al.* 1996). At a stand scale invertebrate diversity may reflect floristic diversity because different invertebrates are adapted to feeding on different species of plant (Recher *et al.* 1996). Plant phenology also influences the abundance and diversity of invertebrates, with many invertebrate taxa responding to periods of new leaf production and flowering (Majer *et al.* 1997)

Four habitat components have been used to characterise the resources used by invertebrates:

1) <u>Overstorey foliage and flowers;</u> a source of edible leaf material, leaf sap, nectar and pollen and shelter sites within foliage;
2) <u>Bark;</u> for shelter and food resources such as litter, exudates and prey;

3) Shrubs and ground vegetation; for foliage and flower resources, and as attachment points for web building spiders.
4) Litter and woody debris; for food and prey and the provision of shelter and a suitable micro-climate

The removal or simplification of some, or all, of these habitat components can reduce invertebrate richness and abundance (Bauer *et al.* 2000). However a number of invertebrate species such as ants, cockroaches and beetles may respond positively to habitat simplification (Abensperg-Traun 1996), such as the creation of canopy and understorey openings which increase ground insolation levels (Oliver *et al.* 2000, Andersen 1986). Invertebrate diversity is therefore likely to be greatest in heterogeneous habitats containing a variety of structural arrangements, ranging from open areas beneath overstorey trees to dense thickets of tall shrubs.

The structural attributes which have been used to quantify invertebrate habitat components are listed in Table 9. The individual habitat components are discussed below.

Table 9: Structural attributes positively associated with either the presence, abundance or richness of one or more orders or species of invertebrates in eucalypt forests (F) or woodlands (W). (-) indicates a study which reported a negative association for some orders.

Attribute	**Study**
% cover of overstorey (F)	York 2000
Number of overstorey stems (F)(W)	Oliver *et al.* 2000, Bromham *et al.* 1999
Eucalypt subgenera (F)(W)	Woinarski *et al.* 1984
% cover of subcanopy (F)	Oliver *et al.* 2000
% cover shrubs or other abundance measure (F)	York 2000, Bromham *et al.* 1999
Measure of litter abundance (% cover, weight, volume, depth) (F)(W)	York 2000, Oliver *et al.* 2000, Bromham *et al.* 1999, Apensberg-Traun *et al.* 1996, Uetz 1990[A]
% cover of lichens (W)	Apensberg-Traun *et al.* 1996
% cover bare ground (F)(W)	Oliver *et al.* 2000, Bromham *et al.* 1999 (-)

[A] Data from Nth American temperate forests

3.8.2 Invertebrate habitat components

OVERSTOREY FOLIAGE AND FLOWERS

The foliage and flowers of eucalypt forests and woodlands support some of the richest invertebrate communities in the world (Majer *et al.* 1997). Recher *et al.* (1996) recorded 976 species of canopy invertebrates on two eucalypt tree species in southeast Australia, and 683 species on two tree species from southwest Australia. Increasing diversity and abundance of invertebrates has been correlated with increasing foliar nutrient concentrations (Recher *et al.* 1996). At the level of subgenus this results in *Symphyomyrtus* species having significantly richer invertebrate assemblages than *Monocalyptus* species. Woinarski and Cullen (1984) found that *Symphyomyrtus* species had six times the densities of lerp forming psyllids, and two times the density of total invertebrates when compared to *Monocalyptus* species.

Significant differences in arthropod composition may also occur between different eucalypt species or between trees of the same species (Majer *et al.* 1997). This reflects differences in the type and quantity of foliage produced (Recher *et al.* 1996), in the timing of flowering and leaf production (Majer *et al.* 1997, Recher and Cullen 1984), and in the association of some invertebrates with particular plant species. For example, the larvae of some butterflies feed on the leaves of particular mistletoe species, which in turn parasitise particular eucalypt species (Woodgate *et al.* 1994). Overstorey species richness, the distribution of basal area amongst overstorey species and tree dbh are attributes likely to describe foliage and flower resources for invertebrates. However to date no study has correlated these attributes with invertebrate abundance or richness.

SHRUBS AND GROUND VEGETATION

Shrubs and ground vegetation provide foliage and flower resources, which may be critical for the juvenile or larval stage of many invertebrates (Candusio 1996). Shrubs also provide attachment points for web-building spiders (Candusio 1996, Uetz 1990). Greenstone (1984) found that as the diversity of the shrub layer increased so did the potential number of attachment points for webs, thereby increasing the diversity of web building spiders. Attributes such as percentage cover of shrubs, and number of shrubs, are direct measures of the shrub resource and have been significantly related to invertebrate diversity (York 2000, Bromham *et al.* 1999). Lichen cover and percentage cover of bare earth are indicative of the development of ground vegetation and have also been significantly related to invertebrate abundance (Oliver *et al.* 2000, Bromham *et al.* 1999, Apensberg-Traun *et al.* 1996).

BARK

The bark of eucalypt forest and woodland trees supports a rich invertebrate fauna, with up to 300 species of invertebrates having been associated with the bark of a single eucalypt tree (Recher *et al.* 1996). The abundance and richness of bark invertebrate communities differs between tree species reflecting differences in bark type and tree phenology (Dickman 1991). In gum barked eucalypt species invertebrate abundance fluctuates seasonally in response to bark shedding, whereas more stable populations are maintained year round on rough barked species (Dickman 1991). Within the same tree species the richest invertebrate communities have been associated with large trees reflecting their complex bark structure and large surface area of bark (Recher *et al.* 1996). Attributes likely to characterise bark resources are the distribution of basal area amongst overstorey species, and mean dbh. However no studies appear to have correlated these, or any other measures of bark resources with invertebrate abundance or diversity.

LITTER

The constituents of litter - leaves, branches, logs and bark - provide food and shelter resources for a distinct invertebrate fauna (Majer *et al.* 1997). This ground fauna includes collembola and acarina species which feed on decomposing plant material (Majer *et al.* 1997, Candusio 1996), and which have been shown to increase in abundance with development of the litter layer and increasing soil organic matter (Majer *et al.* 1997). These detrivores may in turn support a diversity of predator invertebrates including centipedes and spiders for which litter complexity is also critical. Several studies in deciduous temperate forests have correlated spider species richness with litter depth and complexity, indicating that spider habitat increases as the abundance and diversity of spaces within the litter increases (Uetz 1990).

Complexity of litter reflects the diversity of plants contributing material to the litter layer. Andersen (1986) found that the complex and dense litter produced by woodland vegetation supported significantly more individuals and species of ant than the more uniform litter produced in adjacent heath. Similarly Martin and Major (2001) found that litter components in woodland were more diverse than in pasture and that this in part explained the increased abundance of wolf spiders in the woodland. Attributes such as the number of overstorey trees, the number of shrubs and the percentage cover of ground vegetation will be indirect measures of litter abundance and complexity and have in turn been associated with the diversity of ground invertebrates (Bromham *et al.* 1999).

A reduction in the abundance and richness of overstorey or understorey plants is likely to reduce the abundance of litter and the variety of food and habitat resources that litter provides (Andersen 1986). Loss of plant and litter cover may also leave the ground less sheltered reducing the availability of ground moisture. These conditions can lead to significant losses in invertebrate abundance and richness (Bromham *et al.* 1999, Holt *et al.* 1988). However for some invertebrate communities such as ants, overall species richness may be maintained by the addition of new species not present on sites with a well developed litter layer (York 2000). These invertebrate species respond to increased ground insolation and the presence of patches of bare earth.

3.9 Synthesis: a core set of structural attributes

3.9.1 Generic attributes

In this section the various attributes identified for each of the different faunal groups in sections 3.2-3.8, are combined to produce a single set of attributes. This core set of attributes provides a basis for characterising the habitat requirements of all faunal groups, and hence also for characterising the biodiversity value of a particular stand of vegetation. To produce the core set similar attributes have been combined, and are represented by a single generic attribute. For example the attributes, “percentage cover of litter layer”, “litter depth”, “litter biomass”, and “litter volume” are all combined under the generic “percentage cover or other measure of litter abundance”. In this example “abundance of litter” is the key attribute, while the fact that different studies have quantified it in a number of ways is of secondary importance. Similarly the various indices of decorticating bark used by different studies are combined under the single attribute “abundance of decorticating bark”.

The core set of attributes is presented in Table 10. The shaded boxes in this table indicate which faunal groups were significantly associated with a given attribute. This information could provide a basis for ranking attributes in terms of their value as biodiversity indicators, with attribute value increasing with the number of faunal groups in which an association was observed. However, this approach was not adopted for two reasons:

a) Not all faunal groups have been studied with the same intensity, so that the

occurrence of an attribute across only a few faunal groups may indicate a lack of suitable studies, rather than an attribute that is rare or relatively unimportant.
b) An attribute may define part of a niche utilised by members of a given faunal group, so that the presence of a number of rare attributes may be critical to sustaining a diversity of faunal species.
All attributes forming the core set were therefore accepted as potentially important for characterising the structure of Australian forests and woodlands. However, it should be possible to steamline this core set on the basis of predicted or established correlations between attributes.

3.9.2 Eucalypt forest and woodland structural layers

The core attributes in Table 10 also indicate that temperate eucalypt forests and woodlands can be characterised in terms of five distinct structural layers: the overstorey, mid-storey, shrub layer, herb layer and ground layer. For dry sclerophyll communities these layers tend to reflect different life-forms (trees, shrubs, grasses and herbs, and woody debris) rather than different shade tolerances within the same life-form. Such a structural arrangement is consistent with the shade intolerant nature of the eucalypts and their relatively open crowns which maintain a well lit understorey (Florence 1996). This situation contrasts with late successional coniferous forests, and some wet sclerophyll eucalypt forests, which may develop a continuous canopy from ground to canopy top, reflecting the presence of trees of different shade tolerances (eg. Franklin *et al.* 2002).

To complete this review of structure as an indicator of biodiversity, the next and final section discusses approaches which have been used to combine structural attributes in an index of structural complexity.

Table 10: Summary of attributes significantly associated with the presence or abundance of major faunal groupings in eucalypt forests (F) or woodlands (W)

Stratum	**Attribute**	Birds	Arboreal marsupials	Ground mammals	Bats	Reptiles	Amphibians	Invertebrates
Overstorey	Number of overstorey stems (F)(W)	■						■
	Number or basal area of large trees (F)		■					
	Overstorey dbh (F)				■			
	Basal area of overstorey stems (F)(W)	■	■	■				
	Overstorey diversity or species richness (F)	■	■					
	Eucalypt species richness (F)		■					
	Species distribution amongst eucalypt subgenera (F)(W)							■
	Abundance of flowers (F)	■	■					
	Abundance of decorticating bark (F)	■	■					■
	Measures of foliar nutrients (F)(W)	■	■					
	Dbh distribution amongst overstorey species (F)				■			
	% cover canopy trees (F)(W)	■	■	■				■
	Canopy height (F)(W)	■	■		■			
	Canopy surface area and volume (F)(W)	■						
	Maximum dbh unburnt trees (F)				■			
	Number of hollow bearing trees (F)	■	■					
	Abundance of large dead trees (F)					■		
	Mean dbh of dead trees (F)					■		
	Spatial distribution of hollow bearing trees (F)		■					
Mid-storey	Mid-storey height (F)				■			
	Canopy – mid-storey height difference (F)				■			
	% cover of mid-storey (F)	■		■	■			■
Shrub layer	Shrub species richness (F)(W)	■		■		■		
	% cover shrubs or other abundance measure (F)(W)	■	■	■	■	■		■
	Vertical density of shrub layer foliage (F)			■				
	Basal area of acacia species (F)(W)		■					
Herb layer	% cover herbs and grasses (F)(W)	■			■	■	■	
	% cover of lichens (W)					■		■
Ground layer	% cover or other measure of litter abundance (F)(W)	■		■	■	■	■	■
	% cover or other measure of log abundance (W)	■		■		■	■	
	% cover bare ground (F)(W)					■	■	■
	% rock cover (F)					■		
	% cover of debris (litter, logs and rocks) (F)			■				

4. Stand level indices of structural complexity

4.1 Overview of indices

A stand level index of structural complexity is a mathematical construct which summarises the effects of two or more structural attributes in a single number or index value. It is anticipated that if properly designed such an index could function as a reliable indicator of stand level biodiversity (eg. Neumann and Starlinger 2001, Lahde *et al.* 1999, Van Den Meersschaut and Vandekerkhove 1998, Koop *et al.* 1994). Some authors have used a diversity measure, such as the Shannon-Weiner index to quantify a single attribute and have then termed this attribute an index of structural complexity, when in fact they have quantified only one of many possible attributes (eg. Gove *et al.* 1995, Buongiorno *et al.* 1994). In this review such measures are not treated as indices of structural complexity, and are discussed in parts 2 and 3 under the particular attribute they quantify.

Designing an index of structural complexity involves three key steps:
1. Selecting the number and type of attributes to be used in the index. This is not a trivial task because, as parts 2 and 3 of this review have demonstrated there is a wide variety of potential attributes.
2. Establishing the mathematical framework for combining attributes in a single index value.
3. Allocating a score or weighting to each attribute in the index.

There is little consensus in the literature as to how to approach these three steps, and few studies provide a clear rationale, other than the operation of expert opinion, for the selection of particular attributes in preference to others, or for the weighting of attributes. There is also a tendency for researchers to tailor indices to suit their immediate research needs (eg Newsome and Catling 1979), available data (Acker *et al.* 1998), and forest type (eg Koop *et al.* 1994). As a result the literature contains a variety of different indices with no single index preferred over the others.

The most prominent of these indices are summarised in Table 11, and described in more detail in the following sections. For this purpose, indices have been grouped according to the mathematical framework which underpins the index.

Table 11: Indices which have been used in the international and Australian literature to quantify structural complexity.

Index	Number of attributes	Comment
Structural Complexity Index (Barnet *et al.* 1978)	4	Additive index. Attributes describe small mammal habitat.
Habitat Complexity Score (Newsome and Catling 1979^A, Freudenberger 1999^B)	5^A, 6^B	Additive Index. Attributes describe small mammal habitat^A, or bird habitat^B..
Old-growth Index (Acker *et al.* 1998)	4	Measures degree of similarity to old-growth Douglas-fir conditions.
LLNS Diversity Index (Lahde *et al.* 1999)	8	Distinguishes successional stages of Finnish boreal forests.
Biodiversity Index (Van Den Meersschaut and Vandekerkhove 1998)	18	Used to characterise biodiversity in Belgium forests. Attributes benchmarked against reserves.
Vegetation Quality Index (NRE 2001)	11	Attributes benchmarked at the scale of Ecological Vegetation Class.
Rapid Ecological Assessment Index (Koop *et al.* 1994)	9	Attribute levels benchmarked against unlogged natural forest.
Extended Shannon-Weiner Index (Staudhammer and Lemay 2001)	3	Uses an averaging system to extend the Shannon-Weiner Index to height, dbh and species.
Index of Structural Complexity (Holdridge 1967, cited in Neumann and Starlinger 2000)	4	Based on traditional stand parameters, which are multiplied together. Sensitive to number of species.
Stand Diversity Index (Jaehne and Dohrenbusch 1997, cited in Neumann and Starlinger 2000)	4	Combines measures for the variations in species, tree spacing, dbh and crown size.
Structural complexity Index (Zenner 2000)	2	Measures height variation based on tree height and spatial arrangement of trees
STVR (Staudhammer and Lemay 2001)	2	Based on covariance of height and dbh. Independent of height or dbh classes.

4.2 Additive indices based on the cumulative score of attributes

In the literature this is the most straightforward means of constructing an index. A set of attributes is selected, with each attribute contributing a certain number of points to the index. The value of the index is simply the sum of the scores of the attributes. In this approach the contribution of each attribute is easy to assess, and the final value of index relatively simple to compute. However the additive nature of the index can also mask important differences between stands. For example two stands can have the same index value, but this may be the result of quite different combinations of attribute scores.

One of the earliest and simplest additive indices was developed by Barnett *et al.* (1978) to incorporate the structural attributes important to Australian ground dwelling mammals into a single measure. They suggested an index of structural complexity based on four attributes, ground vegetation cover(<1m), shrub cover (1-2m), log cover, and litter cover. Attributes were assessed visually and then scored 0-3 on the basis of cover classes. Scores were then summed to give an index of structural complexity. The abundance of a variety of small mammal species was subsequently correlated with this index (Barnet *et al.* 1978).

Newsome and Catling (1979) extended this approach to include the attributes of tree canopy cover and soil moisture. Their index, or Habitat Complexity Score (HCS), has also been correlated with the abundance of ground dwelling mammals (Catling *et al.* 2000, Catling and Burt 1995), and in a modified form with bird species richness (Freudenberger 1999). HCS has also been suggested as a means of quantifying habitat heterogeneity. A large variance in habitat complexity scores would be indicative of forests with high levels of heterogeneity, whereas clumping of scores about a small variance would indicate a more uniform forest structure (Catling and Burt 1995).

Acker *et al.* (1998) used an additive index to characterise Douglas-fir stands in Western Oregon and Washington. They termed their index an old-growth index (I_{OG}) *because* it measured the dissimilarity to young stand conditions. The index was based on four attributes considered by Spies and Franklin (1991) to successfully discriminate between age classes of Douglas-fir:

- Standard devation of tree dbh
- Number of large (>100cm dbh) Douglas-fir trees
- Mean tree dbh
- Number of trees > 5cm dbh

Attributes describing dead wood (eg. stags and logs), the density of shade tolerant tree species, and the degree of layering in the forest canopy were not included in the index, despite Spies and Franklin (1991) having demonstrated their importance as structural attributes. This was because measurements of these attributes had not been made over the lifetime of the permanent plots used in the study.

Of the four attributes used, each contributed 25% to the value of the index, which was computed as follows: $I_{OG} = 25\Sigma[(X_{i\ obs} - X_{i\ young}) / (X_{i\ old} - X_{i\ young})]$ Where i = 1 to 4, representing each of the four structural variables, $X_{i\ obs}$ is the observed value of the ith structural variable, $X_{i\ young}$ is the mean value of the ith structural variable for young stands, and $X_{i\ old}$ is the mean value of the ith structural variable for old-growth stands.

I_{OG} varies from 0 for a typical young stand, to 100 for a typical old-growth stand. Acker *et al.* (1998) successfully used the change in I_{OG} with time to quantify the rate of development of old-growth conditions in Douglas-fir forests.

Lahde *et al.* (1999) developed an additive index, called the LLNS diversity index, to characterise the structure of boreal forests in Finland. The authors considered variation in tree species and sizes, and the presence of dead standing and fallen trees to be key structural elements. They described these in terms of 8 attributes:

1. The size class distribution of different tree species, with larger size classes in rarer species attracting a higher score;
2. The basal area of trees with dbh > 2cm;
3. The volume of standing dead trees;
4. The volume of fallen dead trees;
5. The density of seedlings;
6. The % cover of understorey plants;
7. The occurrence of special trees (rare because of their size or species);
8. The volume of charred wood with diameter > 10cm.

Attributes were quantified on the basis of classes (eg. dbh class, volume class, density class), with different classes attracting different proportions of the total possible score allocated to the particular attribute. The value of the index was the sum of scores for each of the 8 attributes. Using data from the third National Forest Inventory of Finland, Lahde *et al.* (1999) found that their LLNS index distinguished between successional stages and site types of boreal forest more successfully than either the Shannon-Weiner or Simpson Indices of species diversity.

A more elaborate additive index was developed by Van Den Meersschaut and Vandekerkhove (1998) in order to characterise biodiversity within Belgium forests. They used 18 attributes in their index to describe elements of the overstorey, herb layer and dead wood, and also to reflect parameters considered to be most affected by forest management. The selection and

weighting of attributes were determined by a consensus of experts, and benchmark values for each attribute were based on an analysis of Belgium forest reserves judged most representative of the condition of natural forest stands. The maximum score for the index was 100, with points allocated to attributes as follows:
Overstorey attributes (45); canopy cover (4), stand age (7), number of canopy layers (4), number of tree species per unit area (5), number of native tree species (5), standard deviation of dbh (6), number of large trees (10), presence of natural regeneration (4).
Herb layer composition (25); number of vascular plant species (10), degree of rareness (7), abundance of bryophytes, total cover of herb layer (3).
Dead wood (30); basal area of stags (4), number of large trees (dbh>40cm) (6), total length of large logs (7), range of log diameter classes (8).

Van Den Meersschaut and Vandekerkhove (1998) considered their index to successfully distinguish between a range of forest stands in Flanders, and to have ranked them in a logical order in terms of potential biodiversity value. This was partly attributed to the difference between the maximum and minimum index value, which was equivalent to 1/3 of the maximum score and left sufficient space to determine the biodiversity status of all the stands.

The Victorian Department of Natural Resources and the Environment have used a similar approach to Van Den Meersschaut and Vandekerkhove (1998) in the development of a vegetation quality index to quantify the habitat value of remnants of native vegetation (NRE 2001). The index is additive, and where possible uses natural vegetation to benchmark values for the various attributes. However, unlike Van Den Meersschaut and Vandekerkhove (1998) attributes are benchmarked at the scale of Ecological Vegetation Classes (EVC), so that stands from different EVCs are assessed in terms of different benchmarks. The index also contains a landscape component, which accounts for 25% of the total score.

The attributes and their weighting in the final index value of 100 are as follows:
Stand structural complexity (75): assessed in terms of large trees (10), canopy cover (5), abundance and richness of lifeforms in the understorey (25), litter cover (5), length of logs >20cm diameter (5), regeneration (10) cover of weeds and weed species present (15)
Landscape context (25): assessed in terms of patch size (10), proportion of landscape covered by neighbouring remnants (10) distance to core area of habitat (5).

4.3 Indices based on the average score of groups of attributes

An alternative to simply adding attributes to produce a final score is to find the average score of groups of attributes. Koop *et al.* (1994) used this approach to develop an index for the rapid ecological assessment of Sumatran rainforest. Attributes were placed in three groups, considered to characterise different elements of ecosystem integrity. The groups and their attributes were:

1. Forest overstorey: described by basal area, presence of large trees, maximum tree height, the number of distinct canopy layers, and the form of the diameter distribution (reverse J or other).
2. Light transmission: described the abundance of pioneer species, the richness of light demanding species, and the richness of exotic invader species.
3. Atmospheric moisture: described by the presence of groups of species which indicate high humidity.

For each group attribute scores were tallied to give a score (D) which was compared to benchmarks (R) established in unlogged forest. This allowed a relative score S = (D/R) x 100, to be calculated for each group. The three relative scores were then averaged to give a final score. Koop *et al.* (1994) termed this index a measure of forest integrity because it compared attribute levels to those expected in a natural forest.

Staudhammer and Lemay (2001) used an averaging system to quantify three attributes (diameter, height and species) with the Shannon-Weiner Index instead of the usual one. To do this individual values for the Shannon-Weiner index were calculated on the basis of height classes, dbh classes and species. The three indices were then summed and averaged to give a final value reflecting all three attributes. Staudhammer and Lemay (2001) also applied the Shannon-Weiner index directly on the basis height x dbh x species classes. Both approaches were judged successful in ranking a set of test stands in a logical order reflecting overall biodiversity.

4.4 Indices based on the interaction of attributes

In this approach attributes are combined in an index in a non-linear fashion. The simplest method is to multiple attributes to give the final index value. Holdridge (1967 cited in Neumann and Starlinger 2001) used this technique to combine traditional stand parameters in an index of structural complexity (HC) where HC = $H \times BA \times n \times N$ H is the top-height, BA the basal area, n the number of stems per ha, and N the number of species. Neumann and Starlinger (2001) criticised this index on the basis that it is strongly influenced by the number of species and contains no information on within stand variation.

Jaehne and Dohrenbusch (1997 cited in Neumann and Starlinger 2001) partly address these issues by combining measures for the variations in species composition, diameter, tree spacing, and crown dimension in their Stand Diversity Index (SD), where:
SD = (species variation) x (dbh variation) x (tree spacing variation) x (crown variation)

Neumann and Starliger (2001) found that HC and SD were both useful in characterising the structure of stands across a range of Austrian forest types. HC and SD were significantly correlated with each other and with the standard deviation of dbh. SD was also significantly correlated with overstorey species diversity.

Zenner (2000) constructed a Structural Complexity Index based on the interaction between tree height and the spatial location of trees. To do this, trees were represented as three dimensional data points, with the x, y coordinates representing horizontal position, and the z coordinate representing height. Groups of three adjacent points in this x, y, z space were connected to form a network of non-overlapping triangles. An index of tree height variation was then defined as the sum of the surface areas of these triangles divided by the horizontal area covered by the triangles. Zenner (2000) ambitiously termed this index a Structural Complexity Index (SCI), although it quantified only two of many attributes of structure. The index equates increased structural complexity (higher index values) with increasing tree density and height variation. Canopy gaps are not recognised as increasing structural complexity, because these reduce the value of the index. The index has limited practical value because it requires the position and height of each tree to be precisely determined.

Finally, Staudhammer and Lemay (2001) have proposed an index based on the covariance of dbh and height. The rationale for this index was that unlike the Shannon-Weiner index it would be independent of height or dbh classes. However the index is complex to compute, and only reflects two attributes. It was also the least preferred of the 4 indices tested by Staudhammer and Lemay (2001)

4.5 Conclusions

None of the indices described above is a role model for developing an index of structural complexity. However, taken as a group the indices provide some useful guides in approaching this task.

First, there are clear advantages in using a simple mathematical system to construct an index. This facilitates the use of multiple attributes and also makes it easier to visualise the output from the index in terms of real stand conditions. For example, compare the simple additive index of Van Den Meersschaut and Vandekerkhove (1998), which utilises 18 attributes, to the complex index developed by Staudhammer and Lemay (2001) based on the covariance of two attributes.

Second, there are advantages in benchmarking attributes against their values in natural stands (eg NRE 2001, Koop *et al.* 1994). Using this approach, vegetation communities with naturally simple structures (eg. grassy understorey compared to understorey of herbs and shrubs) can achieve high scores on an index. This approach acknowledges that structural complexity is a relative, rather than absolute concept, and that uniformly high structurally complexity will not necessarily maximise biodiversity. This is because the presence of stands with naturally simple structures can increase the variety of habitats in the landscape.

Third, an index should be based on a comprehensive set of attributes. Relatively few indices currently do this. This largely reflects the arbitrary manner in which attributes are selected. Most studies establish an attribute set by combining attributes the authors consider to be indicative of structure, or biodiversity. How many attributes are included in this set appears to be a matter of subjective judgement, in which the number and type of attributes can vary considerably (see Table 11). The use of an alternative, “reductionist” approach could provide a more objective attribute set. In this approach a large initial set of attributes is established - for example by using attributes identified in Tables 1 and 10 of this review. This set is then reduced to a core set by establishing correlations or other relationships between attributes.

As a final point, the weighting of attributes should be carefully considered as part of the index design. Unfortunately the literature provides little guide as to how do this, other than attempting to weight the contribution of attributes evenly (eg. Acker *et al.* 1998, Koop *et al.* 1994). An iterative approach which trials different weightings seems the most sensible option. The weighing system that most clearly distinguishes between stands could then be adopted.

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Appendix 1.

Summary of studies undertaken in southeast and southwest Australia in which the presence or abundance of different fauna have been significantly associated with vegetation structural attributes, BA = basal area, No. = No., %cover = percentage cover)

Author	**Canopy**	**Trees**	**Shrubs**	**Ground Herbage**	**Hollows**	**Fine litter**	**Coarse debris**	**Rocks**	**Other**
Abbott 1976 Birds (SW WA)									Foliage height diversity*
Abensperg-Traun *et al.* 1996 Arthropods (Gimlet Woodland WA wheatbelt)		No stems	%cover	Lichen crust* Weed cover*		Index (depthxcover)	Index* (no. pieces) Length logs		No. sheep pellets*
Andersen *et al.* 1986 Ants (Heath and woodland SE VIC)		Species	Species			Weight Components			
Andrews *et al.* 1994 Vertebrate fauna (Eucalypt and rainforest NE NSW)	%cover Height %midstorey cover*	Dbh size class Max dbh unburnt trees* No. euc. species No. bark shedding trees >40cm dbh	%cover	%cover grass* %cover herbs	No. hollow bearing trees No. dead trees (>40cm)	%cover	%cover logs* Length logs*	%cover	%bare ground %fern cover %roots in ground cover Landform
Arnold *et al.* 1987 Vertebrate fauna (Woodland, Mallee, Heath SW WA)	%cover	No. stems Richness Basal Area	Richness* %cover* %horizontal cover	%cover herbs / grass		%cover			%bare ground
Barnett *et al.* 1978 Small mammals (Eucalypt and rainforest NE NSW)			%cover>1m* %cover<1m*			%cover*	%cover logs*		Structural complexity score*
Bauer *et al.* 2000 Vertebrate fauna (Cypress Pine forests SW NSW)	Height %cover No. strata	Eucalypt richness* Dominant age Age classes Cypress dbh Mistletoe infestation	Richness Cover *	%cover grass	No. old-growth eucalypts	%cover	No. logs*		Landform Plant species richness*
Bennett 1993 Ground mammals (Eucalypt forest SW VIC)	%cover	BA live trees No. Stems	Vertical density (1-2m*, 2-3m) Vertical cover diversity	Vertical density* (<1m)		Abundance (index)	Log No.s* (index)		Floristic richness* (All plants >0.5m)
Braithwaite *et al.* 1983 Arboreal marsupials (Eucalypt forest Eden SE NSW)		BA* Floristic diversity* BA Peppermints* BA Gums*			No of trees > threshold diameter				BA low foliage nutrient eucalypts*

Author	**Canopy**	**Trees**	**Shrubs**	**Ground Herbage**	**Hollows**	**Fine litter**	**Coarse debris**	**Rocks**	**Other**
Braithwaite *et al.* 1989 Birds (Eucalypt forest Eden SE NSW)		BA live trees BA all trees*	BA acacia species						Foliar magnesium Index*
Bromham *et al.* 1999 Arthropods (Grey Box Woodland N VIC)		No. stems*	No. stems*	%cover* %cover native grasses %cover exotic grasses		Weight* Density* Volume* %particulate matter*			% bare ground
Brown 2001 Reptiles (Box-Ironbark central VIC)	%cover	Size class Sapling density	%cover* Richness* No. stems* (low and tall*)	%cover herbs / grasses*		%cover* Depth*	%cover Log volume Log No.	%cover	%cover bare ground
Brown *et al.* 1993 Reptiles (Mountain Ash forest VIC)		No. stems Mean dbh	%cover	%cover herbs / grasses*	Stag (density, mean dbh*, height, volume)	%cover Depth*	%cover Log No.* Log surface area Log mean diameter* Log moss cover*	%cover	%cover bare ground %cover stumps
Brown *et al.* 1997 Insectivorous bats (Mountain Ash forest VIC)	%cover* (Upper & mid strata) Height* Crown Separation Ratio*	No stems (Upper & mid strata) No stems >1m* No stems <1m* BA upper stratum			No. stags >1m dbh				
Catling *et al.* 1995 Ground mammals (Eucalypt forest SE NSW)	%cover*	BA live trees*	%cover*	%cover*		%cover as a single attribute*			Moisture rating Habitat Complexity Score*
Catling *et al.* 2000 Ground mammals (Eucalypt forest NE NSW)	%cover*	BA live trees*	%cover*	%cover*		%cover as a single attribute*			Moisture rating* Habitat Complexity Score* Foliage nutrients*
Claridge *et al.* 2000 Bandicoots and Potoroos (Euc forest SE VIC/NSW)	%cover (Euc and non euc)	BA live trees No. Stems	%cover %cover acacia spp.	%cover* (0.5-2m) %grass cover	No. stags	%cover (classes) Depth	%cover No. fallen trees	%cover	Tree fern cover Fern cover Sedge cover

Author	Canopy	Trees	Shrubs	Ground Herbage	Hollows	Fine litter	Coarse debris	Rocks	Other
Davey 1984 Arboreal marsupials (Eucalypt forest SE NSW)	Foliage Biomass Index*	Species	Species						
Dickman 1991 Ground-dwelling mammals (Eucalypt forest SW WA, SE NSW)		Dbh %decorticating bark*			Presence	Leaf litter	Presence of logs		
Duncan 1995 Vertebrate fauna (Eucalypt regrowth E & SE TAS)	%cover Height	BA	%cover height	%cover grass		%cover Depth	%cover logs %cover stumps	%cover	%cover bare ground Insolation
Eyre *et al.* 1997 Yellow-bellied glider (Eucalypt forest SE QLD)	%cover Height	Floristic association* No. stems BA BA bark shedding trees	%cover No. stems No. acacia stems		No. stags* No. live trees with hollows			%cover	
Fanning 1995 Vertebrates (Eucalypt and rainforest NE NSW)	%cover %midstorey cover*		%cover (0.5-3m)	%cover* (0-0.5m)	No. hollow bearing trees*		No. hollow logs	%cover *	
Freudenberger 1999 Birds (Grassy woodlands ACT region)	%cover		%cover (0.5-2m, 2-4m)	%cover		%cover	%cover as a single attribute		Habitat complexity score*
Gilmore 1985 Insectivorous birds (Eucalypt forest/woodland VIC and central QLD)	%cover Height* Volume* Surface area*	No. stems BA Bark index*	%cover			Annual litter fall*			No. of plant species
Hadden *et al.* 1996 Herpetofauna (Buloke Woodlands Vic)			%cover* Richness* Height*			%cover*	%cover logs %cover coarse litter		%cover bare ground soil texture
Hazell et al 2001 Frogs (Woodland/farmland SW NSW)	Area of native canopy cover within 1km radius*			Presence of tussocks in the riparian zone*					%bare ground riparian zone* %waterbody perimeter with emergent veg.*
Hindell *et al.* 1987 Koalas (Mixed eucalypt forest Victoria)		Floristic diversity Species* Height No. stems* Foliage weight*							
Jackson 2000 Mahogany glider, Sugar glider (Eucalypt forest N QLD)	%cover (upper* and mid canopy*)	No. species No. food species		%grass cover					No. grass trees

Author	**Canopy**	**Trees**	**Shrubs**	**Ground Herbage**	**Hollows**	**Fine litter**	**Coarse debris**	**Rocks**	**Other**
Kavanagh 1987 Yellow-bellied glider (Eucalypt forest SE NSW)		Dbh* Flowering index* New leaf index* Bark shedding*							
Kavanagh *et al.* 1990 Greater gliders (Eucalypt forest SE NSW)		Species* Dbh* Flowering Young leaves*							
Laven *et al.* 1998 Birds (Box-Ironbark forest Central VIC)							Log volume (>7.5cm)		Presence of piles of coarse debris*
Lindenmayer *et al.* 1990a, 1990b, 1991a, 1991b Arboreal marsupials (Montane Ash forest VIC)	%cover Height Emergent height (overstorey mid-storey)	BA Dbh Bark index*	%cover BA acacia* No. stems	%cover	No. trees >0.5m dbh No. of hollows per tree* Spacing of trees with hollows*				Slope Aspect* No. tree ferns No. cut stumps
Lunney *et al.* 1988 Large herbivores (Eucalypt forest SE NSW)	%cover		%cover %vertical cover	% cover grass		%cover	%cover logs		
Lunney *et al.* 1988 Gould's long-eared bat (Eucalypt forest SE NSW)		Dbh* Species x size class distribution*							
MacNally *et al.* 2000 **Soderquist *et al.* 2000** Birds and mammals (Box-Ironbark Central Vic)	Height	Size class (BA)* BA dead trees Species distribution	Richness Density %cover (low and tall)	% grass cover	No. Hollow bearing trees Position of hollow	%cover	%cover Log No. Log volume	%cover	% cover bare ground No. stumps No. Wattle stems
Martin *et al.* 2001 Wolf spiders (Cypress Woodland W NSW		Height classes	Height classes	%cover (low, medium, high, very high – grass)		%cover	%cover logs		%cover bare ground
McGoldrick *et al.* 1998 Birds (Eucalypt forest central VIC)		Flowering Index*							
Munks *et al.* 1996 Koalas and Possums (Woodland NW QLD)	Height	BA live trees* Richness* Foliar nutrients	BA acacia spp*						Above ground water* Proximity to creek*

Author	**Canopy**	**Trees**	**Shrubs**	**Ground Herbage**	**Hollows**	**Fine litter**	**Coarse debris**	**Rocks**	**Other**
Newsome *et al.* 1979 Ground mammals (Eucalypt forest, woodland, heath SE NSW)	%cover		%cover	%cover		%cover as a single attribute			Moisture rating Habitat Complexity Score
Oliver *et al.* 2000 Ants / Beetles (Blackbutt and Messmate NE NSW)	%cover (>15m, 5-15m*)	No. stems*	%cover (1-5m)	%cover (<1m)		%cover* Depth* Type	%cover (logs >100mm)	%cover	%cover bare earth* Stems<10cm dbh
Parris and McCarthy 1999 Frogs (Eucalypt forest SE QLD)	%cover Forest type	Presence of palms	Composition of understorey vegetation*						Stream size* Stream substrate
Pausas *et al.* 1995 Arboreal mammals (Eucalypt forest SE NSW)		BAxspecies Size classxspecies Foliage nutrient index* Bark shedding index*			Tree hole index* No. trees>60cm*				
Pearce *et al.* 1994 Helmeted Honeyeater (Eucalypt forest SE VIC)	%cover Height Depth*	No. Stems* No. Dead trees BA live trees Bark index	%cover (0.5-1.3, >1.3m)	%cover (<0.5m)					Above ground water* %cover bare ground Floristic richness (All plants >0.5m)
Recher 1969 Birds (Eucalypt forest and heath SE NSW)		Foliage height profile	Foliage height profile	Foliage height profile					Foliage Height Diversity
Recher *et al.* 1985 Birds (Eucalypt forest and woodland SE NSW/VIC)	Height	Species diversity (Overstorey and midstorey) Foliage height profile	Species diversity Foliage height profile	Foliage height profile					Foliage Height Diversity
Seddon *et al.* 2001 Birds (Woodland central W NSW)	%cover	No. dead trees Richness %cover classes for Callitris spp.	%cover (0-2m, 2-4m) %cover all shrubs (0-4m) CV %cover Richness	%cover grass/herbs	No. tree hollows	%cover debris (leaf litter, logs, branches) No. logs (>5cm)			%cover bare ground (rocks, soil, crytograms)

Author	Canopy	Trees	Shrubs	Ground Herbage	Hollows	Fine litter	Coarse debris	Rocks	Other
Smith *et al.* 1989 Echidnas (Eucalypt forest and pasture NE NSW)		No. stems No. dead trees No. stumps					Length logs >10cm (moveable immovable)		No. potential shelter sites*
Smith *et al.* 1994 (Eucalypt and rainforest NE NSW)	%cover* Height*	Height Age structure Floristic type	%cover Floristic type*	%cover*	No. Hollow bearing trees* No. Stumps	%cover*	Length logs	%cover	%bare ground*(-)
Smith *et al.* 1996 Lizards (Gimlet Woodland WA wheatbelt)		No. stems*	%cover*	Lichen crust Weed cover		Index (depthxcover)	Index* (no. pieces) Log length		No. sheep pellets
York 2000 Ants (Euc forest NE NSW)	%cover* (Insolation)		%cover	%cover*		Litter weight*	Large logs		Soil moisture* Soil hardness