The ecological roles of logs in Australian forests and the potential impacts of harvesting intensification on log-using biota

D. B. LINDENMAYER[1*], A. W. CLARIDGE[2], A. M. GILMORE[1],
D. MICHAEL[1] and B. D. LINDENMAYER[3]

A review is presented of the ecological values of logs in Australian eucalypt forests. Logs are a key component of stand structural complexity and have critical functional roles for forest biodiversity including:- (1) providing nesting and sheltering sites for biota, (2) providing foraging substrates for predators like snakes and predatory invertebrates such as velvet worms, (3) providing basking and hibernation sites for reptiles, (4) facilitating animal movement, (5) providing places for key social behaviours, (6) acting as plant germination sites, (7) providing substrates to promote the growth of fungi, (8) providing mesic refugia for organisms during drought and/or fire, and (9) contributing to heterogeneity in the litter layer and patterns of ground cover. Logs also play significant roles in nutrient cycling in forests.

The role of logs is often ignored in forestry operations, including those where harvesting intensification will occur through the removal of dead and/or "defective" standing trees and logs under the guise of removing so-called waste or logging "residues". Recently proposed intensive large-scale forestry operations in the Australian native forest estate (e.g., biomass burning power plants and charcoal plants) have the potential to reduce stand structural complexity, alter forest ecosystem function and negatively impact upon log-dependent species in those part of the landscape where harvesting takes place. The risks of such impacts have not been adequately measured in Australia, but they need to be addressed urgently. Prescriptions for the retention and future recruitment of logs must be developed to avert possible losses of biodiversity.

INTRODUCTION

FOLLOWING the approval of Regional Forest Agreements (hereafter RFA's) between the Commonwealth and State governments, there has been an expectation in the wood products industry that harvesting practices will become more "resource-efficient". This has been termed the "intensification of harvesting operations" (Bauhaus 1999; Kanowski and Buchy 1999). However, maintaining a balance between the ecological importance and economic benefits of native forests is fundamental to achieving the primary objective of RFA's — "ecologically sustainable forest management" or ESFM, where ESFM is defined as (after Lindenmayer and Recher 1998):-

> *"perpetuating ecosystem integrity while continuing to provide wood and non-wood values; where ecosystem integrity means the maintenance of forest structure, species composition, and the rate of ecological processes and functions within the bounds of normal disturbance regimes".*

As part of the proposed intensification of harvesting operations, more "defective trees" and more "waste material" from the forest floor will be taken for use in woodchipping and other types of logging operations. Given proposals for the intensification of forestry practices (Connell *et al.* 1999), in this paper we examine the role and importance of logs for a range of aspects of the ecology and management of Australian eucalypt forests. We considered that an examination of the ecological roles of logs was important because some authors have calculated that dead wood (including logs) provides habitat or has other functions for more than 20% of all forest-dependent organisms worldwide (Hunter 1990; Grove 2001a). A focus on Australian eucalypt forests was chosen because forests outside the reserve system are being targeted for new, large-scale industrial projects such as charcoal-making factories (Environmental Resources Management Australia 2001; Leech 2001) and biomass burning plants for power generation.

Although some of the ecological functions of logs have previously been documented, in part, by other authors (e.g., Dickman 1991), they require current synthesis and appraisal in an Australian forest context. Much of our focus is on logs and biodiversity, but other roles of logs are also highlighted such as their importance as a key structural attribute of native forests. We have not included woodlands and rainforests in this review, although we acknowledge the importance of logs in those ecosystems (e.g., Recher 1985; Grove 2001a, 2002). Part of our examination draws upon published research from overseas, particularly the Pacific Northwest

---

[1] Centre for Resource and Environmental Studies, The Australian National University, Canberra, Australian Capital Territory, Australia 0200.
[2] New South Wales National Parks and Wildlife Service, Threatened Species Unit, Southern Directorate, P.O. Box 2115, Queanbeyan, New South Wales, Australia 2620.
[3] 17 Monkman Street, Chapman, Australian Capital Territory, Australia 2611.
[*] To whom correspondence should be addressed.

PACIFIC CONSERVATION BIOLOGY Vol. 8: 121–40. Surrey Beatty & Sons, Sydney. 2002.

of the U.S.A. (e.g., Maser and Trappe 1984; Harmon *et al.* 1986; Maser *et al.* 1988) and to a lesser extent from Scandinivia (e.g., Berg *et al.* 1994; Bader *et al.* 1995; Sverdrup-Thygeson 2001). This information is relevant since the ecological values of logs in other regions are likely to be broadly equivalent to those in Australian eucalypt forests.

DEFINING LOGS AND PROCESSES LEADING TO THEIR RECRUITMENT

Our definition of logs encompasses not only trees and other woody plants that fall to the forest floor, but also large fallen branches and other woody debris that have been shed or lost from standing living and dead trees. We do not make a distinction between logs and large fallen branches because, as outlined below, both may have a range of broadly similar ecological roles.

Several processes contribute to the accumulation of logs to the forest floor. Trees typically pass through a series of stages in their growth and development (Jacobs 1955) and tree death, decay and eventual collapse are key ones (Franklin *et al.* 1987; Peet and Christensen 1987). Many species of trees shed lateral branches as a natural part of growth and development (Jacobs 1955), and self-pruning is well known in many species of eucalypts (Opie *et al.* 1984). Many trees die and collapse well before they reach a stage where they develop cavities — self-thinning is characteristic of many types of eucalypt forest (Jacobs 1955; Ashton 1976). For example, Lindenmayer *et al.* (1990a, 1997) recognized nine stages of development of trees with hollows in Victorian Mountain Ash *Eucalyptus regnans* forests and of these, the last stage corresponded to logs (Fig. 1). Not all trees pass through each of these stages and some will collapse well before the most advanced stages of senescence. This will, in turn, influence the extent of decay in a recently fallen tree. Notably, in a major North American review, Maser *et al.* (1988) noted strong links between the stages of senescence of standing trees and corresponding log decay categories (Fig. 2). It is likely that similar relationships exist in Australian forests, although research is required to explore such patterns.

LOGS AND STAND STRUCTURAL COMPLEXITY

Stand structural complexity is characteristic of all forests (Franklin *et al.* 1981; Berg *et al.* 1994; Catling and Burt 1995; Noel *et al.* 1998) and it embodies not only particular types of stand attributes, but also the way they are spatially arranged (Lindenmayer and Franklin 2002). Structural attributes include:- (1) trees from multiple age cohorts within a stand including large living and dead stems as well as mixtures of ground cover, understorey and overstorey plants, (2) the vertical heterogeneity created by multiple canopy layers, and, (3) large and small diameter logs. This definition makes it clear that logs are a key component of stand structure (Maser and Trappe 1984; Harmon *et al.* 1986; Sollins *et al.* 1987; Niemela *et al.* 1993; Recher 1996; Kaila *et al.* 1997; Lee *et al.* 1997; Lindenmayer *et al.* 1999a).

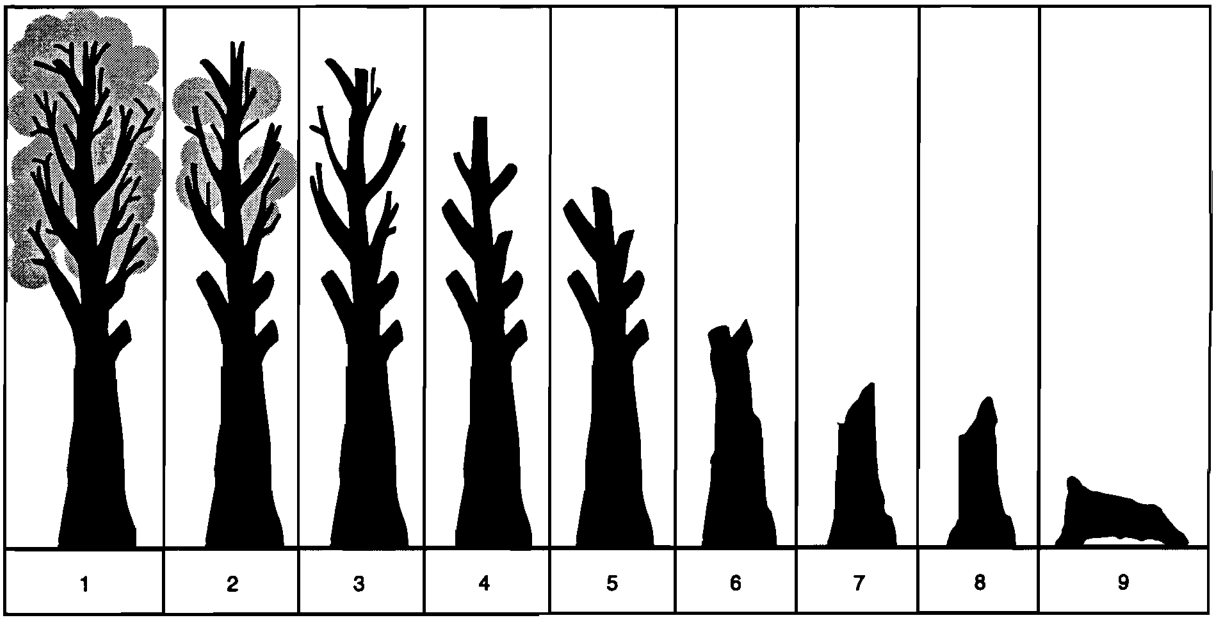

Fig. 1. Decay stages in hollow-bearing Mountain Ash trees in the Central Highlands of Victoria. Logs correspond to trees in decay state 9 (redrawn from Lindenmayer *et al.* 1997).

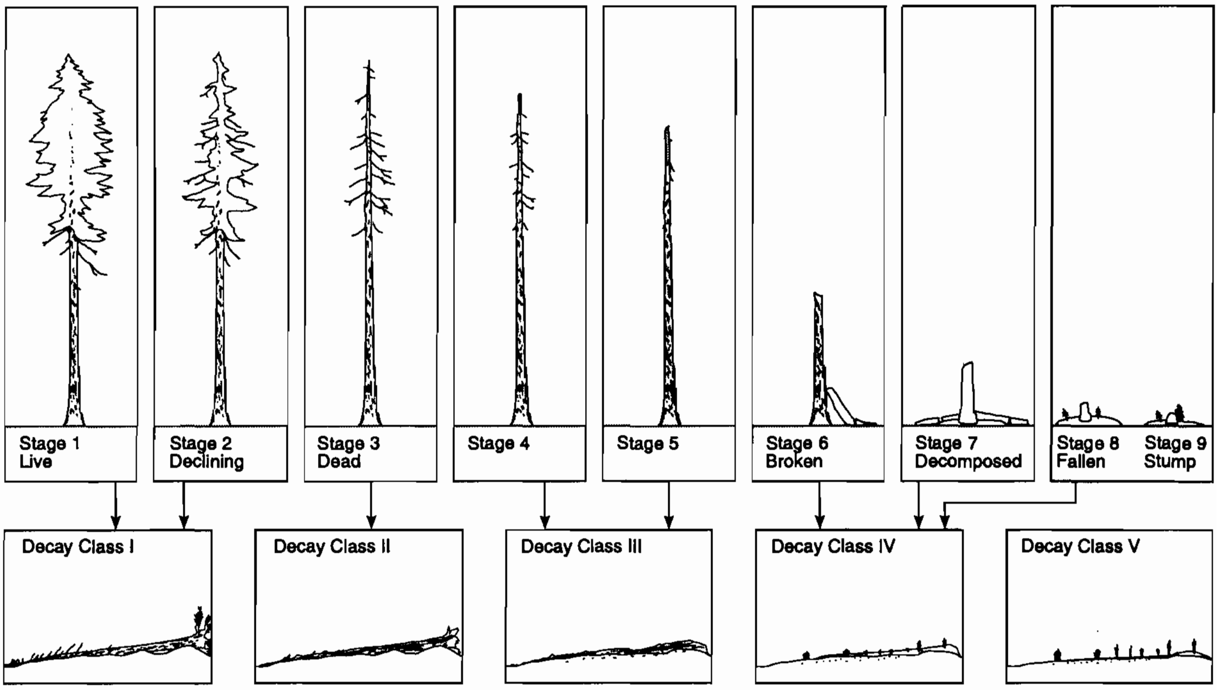

Fig. 2. Relationships between the stage of standing tree senescence and the associated decay status of logs in Douglas Fir (*Pseudotsuga menziesii*) in northwestern North America (redrawn from Maser *et al.* 1988).

Stand structural complexity is important for two key reasons. First, it is well known that structurally complex forests allow the potential for greater inter-specific segregation of resources and microhabitats thereby enabling more species to occur locally (MacArthur *et al.* 1966; Rosenzweig 1995). Second, forests where stand structural complexity has been simplified through intensive management (e.g., Linder and Östlund 1998; Bunnell 1999; Bobiec 2002) have impaired value for biodiversity (Berg *et al.* 1994; Angelstam 1996; Lindenmayer and Franklin 2002). This is because many types of structural attributes can be essential nesting, sheltering and foraging sites for a wide range of species (see below). The loss of key elements of stand structural complexity like large diameter trees (Linder and Östlund 1998; Gibbons and Lindenmayer 2002), thickets of understorey plants (Ough and Murphy 1996) and logs (Smith *et al.* 1992) can:- (1) eliminate organisms from logged areas that might otherwise persist there; (2) prolong the period that logged and regenerated stands are unsuitable habitat for species that have been displaced; (3) impair the dispersal of some animals through logged areas, and, (4) eliminate within-stand variation in habitat conditions required by some taxa.

"NATURAL" QUANTITIES OF LOGS IN FORESTS

There have been few investigations of log volumes in Australian forests. A recent study showed that log volumes were large in Mountain Ash forests — approximately 350 m^3/ha averaged across all age classes, with some old growth stands having volumes in excess of 1 100 m^3/ha (Lindenmayer *et al.* 1999a). Meggs (1996) calculated mean levels of decaying wood in young (5 and 20 year old) Messmate *E. obliqua* forests in Tasmania and also found large volumes of logs (174 to 455 m^3/ha). In drier and less productive forests in southeastern New South Wales, Woldendorp (2000) found the measured biomass of logs in unharvested stands (primarily Brown Barrel *E. fastigata*) varied from 15 to 126 tonnes/ha. Robinson (1997) estimated mean values of logs in River Red Gum *E. camaldulensis* forest to be approximately 125 tonnes/ha.

Few studies in Australia have examined log accumulation rates (but see Robinson 1997). The rate of log decay also has been only rarely quantified and to date there have been just three studies — two from Western Australia (Brown *et al.* 1996; O'Connell 1997) and a third from southeastern Australia which included a major review of the topic (Mackensen and Bauhaus 1999). Log decomposition is significantly influenced by factors such as the presence of termites, log diameter (large logs persist longer than small ones), the position of a log in the landscape, and the durability of the tree species undergoing decay (reviewed by Mackensen and Bauhaus 1999). These influences can lead to markedly different results between studies, even those of the same tree species (compare Brown *et al.* 1996 and O'Connell 1997). Mackensen and

Bauhaus (1999) concluded that the turnover period for logs of most Australian hardwood species (i.e., the time by which 95% of material had been lost) would be at least 25–30 years, although turnover times exceeding 100 years could be expected for more durable species.

In addition to the paucity of data on log accumulation and decomposition, there is also limited information on differences in the volume and decay status of logs in managed and unmanaged forests. A recent study in north Queensland found that log volumes varied from approximately 20 m^3/ha in regrowth tropical rainforest to almost 36 m^3/ha in old growth tropical forest stands (Grove 2001a). The scarcity of logs in these tropical forests was attributed to rapid rates of decomposition (Grove 2001a). Lindenmayer *et al.* (1999a) found significantly larger logs in mature and old growth stands of Mountain Ash than in regrowth stands recovering after logging. However, they detected no significant age class effects on log volume. Lindenmayer *et al.* (1999a) attributed this to biological legacies (*sensu* Franklin *et al.* 2000) such as dead standing trees and logs that remained after previous disturbance events like logging, fires and wind storms in the 20 and 60 year-old regrowth forests they measured. Therefore, important considerations in age class comparisons of logs in environments, such as those in Mountain Ash where stand-replacing fires can occur, are the condition of a stand when it was previously disturbed and the quantity of biological legacies that remain following disturbance. Notably, under present proposals to increase the intensity of forestry practices (Leech 2001), many biological legacies such as standing dead trees and logs would be removed. This is likely to create significant differences in log characteristics between managed and unmanaged forests and comparative studies of the impacts on stand structure are urgently required (see Discussion section below).

Existing knowledge gaps on log volume, accumulation and decomposition are problematic because they make it difficult:- (1) to determine how long it may take to recover to pre-harvesting levels (or other defined levels), and, (2) to plan for ecologically sustainable forest management. These issues are examined further in the Discussion section following an assessment of the role of fallen timber in perpetuating essential ecological and physical processes.

LOGS AND BIODIVERSITY

Logs have many values for forest biodiversity including:- (1) providing nesting and sheltering sites for biota, (2) providing foraging substrates for predators ranging from snakes to velvet worms, (3) providing hibernation sites for biota, (4) providing basking sites for reptiles, (5) facilitating animal movement, (6) providing places for key social behaviours, (7) acting as plant germination sites, (8) providing substrates to promote the growth of fungi, (9) providing mesic refugia for an array of organisms during drought and/or fire, and (10) contributing to heterogeneity in the litter layer and patterns of ground cover. We elaborate on these roles in the following section. We have not differentiated between obligate and facultative log users because there is insufficient available data in Australia to meaningfully do so at present.

Nesting, sheltering and other habitat roles

Logs provide nesting and sheltering sites for many forest-dependent taxa. They provide habitat for numerous species of invertebrates including rich assemblages of detritivores and decay organisms (Taylor 1990; Barclay *et al.* 2000a). Some species of threatened or endangered invertebrates are dependent on logs (Meggs and Taylor 1999). For example, the Threatened Fauna Manual for Tasmania (Forestry Practices Board 1998) listed several threatened forest invertebrates strongly associated with rotting logs including:- Broad-toothed Stag Beetle *Lissotes latidens*, Mt. Mangana Stag Beetle *Lissotes menalcas*, Stimson Stag Beetle *Hoplogonus stimsoni*, Northeast Forest Snail *Anoglypta launcestonensis*, Northwest Velvet Worm *Ooperipatellus cryptus*, Blind Velvet Worm *Tasmanipatus anophthalmus*, and Giant Velvet Worm *Tasmanipatus barretti*.

The importance of logs as nesting and sheltering sites has been well documented for many mammals including the Bush Rat *Rattus fuscipes* (Warneke 1971), carnivorous marsupials such as the Agile Antechinus *Antechinus agilis* and the Eastern Quoll *Dasyurus viverrinus* (Dickman 1991; Godsell 2000), the Numbat (Friend 1990), the Mountain Brushtail Possum *Trichosurus cunninghamii* (Owen and Thomson 1965; Davey 1989; Lindenmayer *et al.* 1990b), and the Echidna *Tachyglossus aculeatus* (Wilkinson *et al.* 1998; Rismiller 1999). Dickman (1991) presented information on a range of ground-dwelling and scansorial forest mammals that use logs for shelter. He showed that logs provide a large proportion of the shelter sites used by species such as the Echidna, the Dusky Antechinus *A. swainsonii*, and the Bush Rat. In many eucalypts, hollows in standing and living dead trees remain suitable for use even after a tree has collapsed (Settle and Croft 1982; Williams and Faunt 1997). Hollows in logs are used as sheltering sites by a wide range of other species such as the Numbat *Myrmecobius fasciatus* (Christensen 1975; Christensen *et al.* 1984; Friend 1990) and the Fawn Antechinus *A. bellus*

(Calaby 1995). A radio-tracking study of the Numbat by Christensen *et al.* (1984) showed that individual animals can use more than 20 different logs as nesting sites or places to shelter when alarmed or disturbed.

Review texts on birds (e.g., Schodde and Tiedemann 1986; Higgins *et al.* 2001) show that logs are habitat components for a range of forest-dwelling birds, although relatively few species use them for nesting (Beruldsen 1986). For example, logs provide roosting and perching sites for a range of ground-foraging species. Laven and Mac Nally (1998) demonstrated that the mean occurrence of a range of bird species was nine times higher in areas with logs than areas where such structural attributes were absent.

Logs provide sites for reptiles to shelter overnight and for them to lay their eggs (Rawlinson 1975; Brown and Nelson 1993; Shine 2001). They are also key winter hibernacula (see below). Many studies have documented strong relationships between logs and the occurrence of some species of reptiles (e.g., Goldingay *et al.* 1996; Hannah *et al.* 1998). Cogger (2000) provided a short description of the "habit" of each reptile species in Australia and logs are listed in these descriptions in a substantial subset of terrestrial taxa. Similar outcomes were obtained from examinations of other works on Australian reptiles (e.g., Wilson and Knowles 1988; Ehmann 1992). Given this information, Table 1 lists some of the reptile taxa from forests in southeastern Australia that are known to be associated with logs.

Foraging substrates

Logs are used for foraging by many invertebrate groups (Taylor 1990; New 1995) such as:- the Onychophora (velvet worms) (Barclay *et al.* 2000a, 2000b), Chilopoda (centipedes) (Lewis 1981; Mesibov 1986), Isoptera (termites) (Fay and Calaby 1970; Perry *et al.* 1985), Blattodea [cockroaches] (Roth and Willis 1960), and Collembola [spingtails] (Greenslade 1985 in Taylor 1990; Greenslade 1990). Logs provide primary habitat for particular stages of the life cycle of several invertebrate taxa; the larvae of lucanid beetles is a classic example.

Invertebrate assemblages that inhabit logs are food for vertebrates. A useful example is the Echidna — a species for which 50% or more foraging observations summarized by Dickman (1991) were from logs. Smith *et al.* (1989) also recorded a large proportion of diggings made by the Echidna from the base of logs. Another example is the Numbat which consumes termites that live in and around rotting logs (Christensen *et al.* 1984). Braithwaite (1979) believed that logs were primary habitat for the invertebrate prey of the Brown Antechinus. Other studies of *Antechinus* spp. in tropical forests of northern Queensland showed that animals can spend substantial periods foraging on small and large diameter logs (Watt 1991). This may account for the strong relationships that have been observed between the occurrence of *Antechinus* spp. and log abundance (Dickman 1980; Statham and Harden 1982; see below).

Logs indirectly provide food resources for mycophagous (fungus-feeding) mammals. They serve as places where hypogeous (underground-fruiting) mycorrhizal fungi develop (see below) and become an important source of food for animals like the Bush Rat, the Southern Brown Bandicoot *Isoodon obesulus*, and the Mountain Brushtail Possum *Trichosurus cunninghamii* (sp. nov) (Claridge and Lindenmayer 1993) and the Mountain Brushtail Possum (Claridge and May 1994; Claridge and Lindenmayer 1998).

Logs are used for foraging by a range of Australian forest birds (reviewed in Schodde and Tiedemann 1986; Higgins *et al.* 2001). A small set of the many possible examples is given below. The diet of the Lyrebird *Menura novaehollandiae* includes a wide range of prey which appear to be strongly associated with logs and deep litter (Lill 1996). Similarly, ground-foraging taxa like the Eastern Whipbird *Psophodes olivaceus* forage around logs and turn over ground litter as part of searching for food (A. Gilmore, unpubl. data). The near-threatened Brown Treecreeper *Climacteris picumnus* forages predominantly on and near the ground and makes extensive use of standing dead timber and logs (Noske 1982; Walters *et al.* 1999). Particular forest types often support a large number of bird species that forage extensively around logs. For example, Laven and Mac Nally (1998) and Mac Nally *et al.* (2001) identified a range of bird taxa strongly associated with logs for foraging or cover in box-ironbark and River Red Gum forests of northern Victoria. These included:- robins *Petroica* spp., Eastern Yellow Robin *Eopsaltria australis*, thornbills *Acanthiza* spp, White-throated Treecreeper *Cormobates leucophaeus* and other species of treecreepers *Climacteris* spp.

Basking and hibernation sites for reptiles

Logs are basking sites for many species of reptiles (Heatwole and Taylor 1987). Webb (1985) showed that several species of forest skinks used logs as elevated perches for basking during early morning and late afternoon. The importance of logs for some heliothermic lizards is reflected in the relative number of observations on such substrates. For example, in the forests of southeastern Australia, more than half of the observations of the following five

Table 1. Examples of reptiles in southeastern Australian forests (distributed between Sydney and Tasmania) that utilize microhabitats such as logs.

Family	Species	Basking/foraging	Sheltering/Over-wintering	Reference
Gekkonidae	*Christinus marmoratus*		x	1,3
	Diplodactylus vittatus		x	1,3
Pygopodidae	*Delma inornata*	x	x	1,3
	Pygopus lepidopodus		x	1
Agamidae	*Amphibolurus muricatus*	x		2
	Physignathus lesuerii howitti	x		1
	Pogona barbata	x	x	1,3
	Tympanocryptis diemensis	x		2
Varanidae	*Varanus rosenbergi*	x	x	1
	V. varius	x	x	1
Scincidae	*Bassiana duperreyi*	x		2
	B. platynota	x		3
	Carlia tetradactyla		x	3
	Cryptoblepharus carnabyi	x	x	1,3
	C. virgatus	x	x	1
	Cyclodomorphus praealtus		x	1
	C. casuarinae		x	1,2
	E. striolata	x	x	1,3
	E. whiteii whiteii		x	1,3
	Eulamprus heatwolei	x		3
	E. kosciuskoi	x	x	1
	E. quoyii		x	1
	E. tympanum	x	x	1,3
	E. tenuis	x	x	1,2
	Hemiergis decresiensis		x	1,3
	Lerista bougainvilli		x	1,3
	Menetia greyii		x	3
	Morethia boulengeri		x	1,3
	Nannoscincus maccoyi		x	1,3
	Niveoscincus coventryi	x	x	1
	Niveoscincus metallica		x	3
	Pseudomoia entrecateauxii	x		1,2
	P. spenceri	x	x	1
	Saiphos equalis		x	1
	Saproscincus mustelinus		x	2
	Tiliqua scincoides		x	1,3
	T. nigrolutea		x	1
	Trachydosaurus rugosa		x	1,3
Typhlopidae	*Ramphotyphlops nigrescens*		x	1,2
Boidae	*Morelia spilota*	x	x	1
Colubridae	*Dendralaphis punctualata*	x	x	1
	Boiga irregularis	x	x	1
Elapidae	*Austrelaps ramsayi*		x	3,4
	A. superbus		x	3
	Cacophis squamulosus		x	1
	Drysdalia coronoides		x	4
	D. rhodogaster		x	4
	Hemiapsis damelii		x	4
	Hoplocephalus bitorquatus	x	x	1,4
	H. stephensii	x	x	1,4
	Notechis scutatus	x	x	3
	Pseudechis porphyriacus		x	3
	Pseudonaja textilis		x	1
	Rhinoplocephalus nigrescens		x	1
	Suta flagellum		x	4
	Suta dwyeri		x	4
	Vermicella annulata		x	4

References 1 = Cogger (2000), 2 = Swan (1990), 3 = Michael (unpubl. data), 4 = Weigel (1990).

species of skinks were recorded on logs:- (1) Southern Water Skink *Eulamprus heatwolei* [88%], (2) Carnaby's Wall Skink *Cryptoblepharus carnabyi* [87.5%], (3) Tree Skink *Egernia striolata* [80%], (4) Spencer's Skink *Pseudemoia spenceri* [78%], and (5) Highland Water Skink *Eulamprus tympanum* [60%] (Webb 1985; Brown and Nicholls 1994; Kutt 1994).

Aggregations of some species over-winter or hibernate deep inside rotting logs. Examples include the Three-toed Skink *Hemiergis decresiensis*, MaCoy's Skink *Nannoscincus maccoyi*, and Coventry's Skink *Niveoscincus coventryi*) (Robertson 1981; Webb 1985; Bennett 1997).

Animal movement

Logs assist the movement of many species. MacEachern (2001) showed how the spatial arrangement of rotting logs strongly influenced the movement of the wood-dwelling native cockroach *Pariesthia australis*. Barclay *et al.* (2000b) suggested that an increased number, length and volume of logs assisted dispersing velvet worms in finding suitable habitat. The runways of many species of terrestrial animals are often along or directly adjacent to logs (e.g., several species of rodents; see Watts and Aslin 1981; Halstead-Smith 1999). Populations of small mammals use windrows of eucalypt logs within otherwise unsuitable areas of exotic softwood Radiata Pine *Pinus radiata* plantations (Friend 1982; Lindenmayer *et al.* 1999b). Curry (1991) found that windrows of eucalypt logs were used as movement conduits by birds in softwood plantations. The Mountain Brushtail Possum uses large logs as movement pathways and is often captured in traps placed on them (Seebeck *et al.* 1984; Lindenmayer *et al.* 1998).

Social behaviour

Logs can be important in the social behaviour of many forest-dependent species. The Common Wombat *Vombatus ursinus* and the Mountain Brushtail Possum deposit scats in prominent places such as logs to signal territory boundaries (Triggs 1997). Braithwaite (1979) found that areas which supported few logs were occupied by subordinate male Brown Antechinus *Antechinus stuartii*. Skinks may aggressively exclude conspecifics from logs used for shelter, basking or foraging (Stamps 1977). Tasmania's Alpine Skink *Niveoscincus microlepidotus* and *Egernia striolata* are two examples (Melville and Swain 1999). Logs are important in the social behaviour of invertebrates. For example, they are sites where male velvet worms release pheromones to attract females thereby helping potential mates to successfully colonize logs (Barclay *et al.* 2000a).

Germination sites for plants

Logs are nursery sites for some species of plants and provide places for the germination and subsequent growth of ferns, mosses and liverworts (Ashton 1986). As an example, logs are listed as a key substrate for the occurrence of more than ten species of mosses and 20 species of liverworts in Tasmanian forests alone (Jarman and Fuhrer 1995). Tasmanian studies have demonstrated the importance of logs in promoting the regeneration of forest trees (Read and Hill 1983; Cullen 1987). McKenny and Kirkpatrick (1999) showed that the seedlings of many tree species were significantly more abundant on logs than adjacent soil. Moss cover also was considerably greater on logs. For example, the rainforest tree Celery Top Pine *Phyllocladus aspeniifolius* preferentially establishes on logs. As logs rot, the expanding root system of seedlings growing on them penetrates the decomposing mulch and extends into the topsoil (Barker and Kirkpatrick 1994). Myrtle Beech *Nothofagus cunninghamii* trees in Victorian forests are believed to undergo similar patterns of germination and early growth with the moisture in rotting logs facilitating access to water for growing seedlings (Howard 1973). Detailed vegetation surveys in Victorian Mountain Ash forests (Lindenmayer *et al.* 2000) found that a range of understorey plant species such as Dogwood *Cassinia aculeata*, Musk Daisy Bush *Olearia argophylla* and Mountain Pepper *Tasmannia lanceolata* germinated on rotting logs.

Clusters of logs can have a protective role for plants sensitive to grazing and browsing by herbivores through limiting physical access by grazing animals such as wallabies (Kirkpatrick 1997). Similarly, they also provide protection to young seedlings and limit damage from bioturbation by mammals and birds (e.g., the Superb Lyrebird) (McKenny and Kirkpatrick 1999).

Substrates to promote the growth of fungi

Logs in various stages of decay are key microhabitats for many species of fungi. For example, Pearce and Malajcuk (1990) recorded more than 80 species of fungi on residual wood in Karri (*Eucalyptus diversicolor*) forests in Western Australia. The habitat value of logs has been particularly well documented for fungi that form macroscopic fruit-bodies (see Maser and Trappe 1984 for a review in a North American context). Cursory examination of Australian mycological field guides reveals that many fungal species fruit only in close association with logs (Table 2). The majority of these fungi form epigeous or above-ground fruit-bodies, and are saprotrophic; i.e., they derive many of their nutrients and energy by utilizing decaying wood.

Table 2. Examples of Australian macrofungi known to utilize logs as primary micro-habitat.

Order	Family	Species	Habit	Nutritional Mode	Reference
Ascomycetes	Leotiaceae	*Chlorocibaria aeruginascens*	E	SAP	I
	Otidaceae	*Scutellinia* aff. *margartiaceae*	E	SAP	1
	Pezizaceae	*Peziza scutelleta*	E	SAP	2
	Xylariaceae	*Daldinia concentrica*	E	SAP	1
Basidiomycetes	Agaricaeae	*Clitocybula* aff. *cyathiformis*	E	SAP	2
	Clavicoronaceae	*Clavicorona piperata*	E	SAP	1
		C. pyxidata	E	SAP	2
	Coniophoraceae	*Podosepula australis*	E	SAP/PAR	1
	Coprinaceae	*Coprinus* sp.	E	SAP	1
		Coprinus disseminatus	E	SAP	2
	Coriolaceae	*Pycnoporus coccineus*	E	SAP	1
		Piptoporus australiensis	E	SAP/PAR	1, 2
		Trametes cinnabarina	E	SAP	2
		T. lilacino-gilua	E	SAP	2
		Trametes versicolor	E	SAP	1, 2
	Cortinariaceae	*Cortinarius* aff. *sanguineas*	E	SAP	2
		Descolea maculata	E	MYC	1
		Gymnopilus austrosapineus	E	SAP	1
		G. penetrans	E	SAP	2
		G. purpurata	E	SAP	2
	Hygrophoraceae	*Hygrophorus minutulus*	E	SAP	2
		Galerina unicolor	E	SAP	1
	Lentinaceae	*Pleurotus nidiformis*	E	SAP	2
	Lycoperdeacaea	*Lycoperdon pyriforme*	H	SAP	2
	Pluteaceae	*Pluteus atromarginatus*	E	SAP	1
		P. cervinus	E	SAP	2
		Volvaria aff. *taylori*	E	SAP	2
	Stereaceae	*Stereum hirsutum*	E	SAP	1, 2
		S. illudens	E	SAP	2
	Strobilomycetaceae	*Fistulina hepatica*	E	SAP	2
		Fistulinella mollis	E	SAP	1
	Strophariaceae	*Hypholoma australe*	E	SAP	1
		H. fasciculare	E	SAP	2
		H. radicosum	E	SAP	2
		H. sub-lateritium	E	SAP	2
		Pholiota multicingulata	E	SAP	1
		P. aff. *squarroripes*	E	SAP	2
		Tubaria rufofulva	E	SAP	1
	Tremellaceaea	*Tremella aurantia*	E	PAR	1
		T. mesenterica	E	PAR	1
		Tremellodon gelatinosporum	E	PAR (?)	2
	Tricholomataceae	*Anthracophyllum archeri*	E	SAP	1
		Armillaria asprata	E	SAP	2
		A. hinnulea	E	SAP	2
		Collybia fuscipes	E	SAP	2
		C. velutipes	E	SAP	2
		Marasmius aff. *cinnamoneus*	E	SAP	2
		Mycena subgalericulata	E	SAP	1,2
		Ompholina chromacea	E	SYM	1
		Omphalotus nidiformis	E	SAP	1
		Panellus ligulatus	E	SAP	1
		Tricholoma rutilans	E	SAP	2
		Tricholompsis rutilans	E	SAP	1
	Xeromaceae	*Boletus ananiceps*	E	SAP	1, 2
	Xylariaceae	*Xylaria polymorpha*	E	SAP	2

Key: Reference; 1 = Bougher and Syme (1998), 2 = Young (1986). Habit; E = Epigeous (above-ground fruit-bodies), H = hypogeous (underground fruit-bodies). Nutritional mode; MYC = Mycorrhizal, SAP = Saprotrophic, SYM = Symbiotic, PAR = Parasitic.

Logs are also microhabitat for a suite of hypogeous (underground-fruiting) fungi, most of which are presumed to be mycorrhizal and are food for many terrestrial mammals (Claridge and Lindenmayer 1993, 1998; Claridge and May 1994). The relationship between these latter groups of fungi and logs is particularly well documented for species in the Pacific Northwest of the United States of America (e.g., Amaranthus *et al.* 1994). As studies of the microhabitat requirements of Australian hypogeous fungi are in their infancy (Claridge *et al.* 2000a, 2000b), the relative value of logs in this country is an important area of future research.

Logs provide suitable substrate for fruit-body production of fungi for several reasons. Firstly, they retain moisture for longer periods than the surrounding soil, thereby protecting fruit-bodies from desiccation (Amaranthus *et al.* 1994). The period of fruit-body production by species associating with logs can be longer than that for other fungal species growing elsewhere. Logs can concentrate mobilized nutrients as they move downslope across or through the soil profile (Maser and Trappe 1984). This is because fungi "scavenge" nutrients from the soil and combine them with energy and nutrients obtained from decomposing logs. In some temperate forest types (such as those in North America), the occurrence and relative abundance of fruit-bodies from hypogeous fungi is higher at sites with large logs than at sites without these features (see Waters *et al.* 1997). Thus, overall forest productivity may be influenced by these key structural attributes.

Mesic refugia

Logs, particularly those in the late stages of decay, often have a high moisture content (Yoneda 1986; Sollins *et al.* 1987). The moisture content of logs can be as high as 350% or more of dry weight (Yoneda 1986; Sollins *et. al.* 1987). For example, in the Mountain Ash forests of Victoria, luxuriant moss mats develop on large logs (Lindenmayer *et al.* 1999a). Ashton (1986) estimated that the dense mats of the mosses *Wijkia* and *Lepidozia* can hold 960% and 990% respectively of their dry weight as water. Considering the enormous log volumes in Mountain Ash forests and that the average moss cover on logs is approximately 20% (Lindenmayer *et al.* 1999a), these moss mats may hold a substantial store of water. This may be valuable for a range of organisms for which moisture conditions are important such as those associated with decomposition components of food webs and nutrient cycles. For example, Brown *et al.* (1996) suggested that the high water content of logs enabled moisture-sensitive organisms to remain active for longer during dry periods. This is particularly relevant to taxa prone to desiccation such as velvet worms (Tait *et al.* 1990). Indeed, Scott and Rowell (1991) found that the water content of decomposing logs was a major determinant of habitat suitability for the velvet worm *Euperipatoides rowelli*.

Logs and heterogeneity in the litter layer

Logs can act as leaf litter "traps" and influence the movement of fine litter through the forest. Such accumulations of litter can be valuable habitats for some species. For example, Andrew *et al.* (2000) found that ant species richness was significantly higher in leaf litter adjacent to logs than in litter accumulations sampled away from logs.

Logs are a source of fuel for forest fires (Luke and McArthur 1978), and this can be important for some elements of biodiversity. Clusters of logs lead to high localized levels of fuel and, in turn, high localized fire intensities. This can suppress the growth of plants such as grasses and benefit other plant taxa sensitive to competition from grasses (Kirkpatrick 1997). Conversely, large logs can act as micro fire-breaks, not only because of their diameter and length but also because of the moisture they contain and moisture levels in the adjacent litter (Andrew *et al.* 2000). The moisture content of logs may explain why they are often not completely consumed in a single fire event. The value of logs as micro-refugia has been demonstrated in several studies. Christensen (unpubl. data) in Christensen *et. al.* (1981) recorded high numbers of skinks that survived under logs in areas burnt by wildfires of moderate to high intensity. Campbell and Tanton (1981) investigated the effects of low intensity fires on soil and litter invertebrates. They found that invertebrates could survive under logs despite the complete consumption of surrounding litter and attributed this to lower fire temperatures and higher moisture levels under logs.

LOGS IN AQUATIC ECOSYSTEMS AND ASSOCIATED RIPARIAN AREAS WITHIN FORESTS

Aquatic ecosystems such as streams and wetlands, as well as the vegetation associated with them (e.g., riparian and floodplain zones), are an integral part of forest ecosystems in all parts of the world (Naiman and Bilby 1998; Lindenmayer and Franklin 2002). A very large proportion of the biodiversity found in forest landscapes is associated with aquatic ecosystems (e.g., Recher *et al.* 1980; Mac Nally *et al.* 2001). Logs provide cover and breeding sites for fish and other aquatic organisms (Koehn 1993; Crook and Robertson 1999; Lovett and Price 1999) and are locations from which many species of frogs vocalize (Barker *et al.* 1995). The structure of aquatic ecosystems within forest landscapes is strongly influenced by the availability of large logs that influence hydrologic and geomorphic processes (Gippel 1995; Gippel *et al.* 1996) and which need to be delivered at appropriate intervals (Beschta and Platts 1986; Maser *et al.* 1988; Maser and Sedell 1994).

LOGS AND NUTRIENT CYCLING, CARBON BUDGETS AND BUFFERS FOR ECOSYSTEM FUNCTIONS

Logs are valuable long-term sources of energy and nutrients in forest and aquatic ecosystems (see Attiwill and Leeper 1987; reviewed by Harmon *et al.* 1986 in a North American context). For example, they can be valuable sites for nitrogen fixation for micro-organisms with nutrients eventually finding their way into the soil (Sollins *et al.* 1987; Lamb 1991). Logs are also critical sites for carbon storage — a key ecosystem service (Harmon *et al.* 1990; Brown *et al.* 1997; Wayburn *et al.* 2000; Harmon 2001a; Martin *et al.* 2001). In forests in southeastern New South Wales, the amount of carbon stored in logs ranged from 15 tonnes/ha to 125 tonnes/ha (mean = 53 tonnes/ha) (Woldendorp 2000). In wetter and more productive Mountain Ash forests in Victoria, where extensive log volume measurements were made (Lindenmayer *et al.* 1999a), old growth stands of Mountain Ash forest were crudely estimated to support up to 350 tonnes of carbon/ha (assuming that logs were, on average, 60% decayed). While some of the carbon in logs is released into the atmosphere during the decay process, some of it is incorporated into the soil as long-lived soil carbon (B. Mackey, pers. comm.).

Logs provide a major nutrient store in forests that is released slowly through decomposition (Krankina *et al.* 1999). Swift (1977) noted there were two key consequences of the high lignin content of wood and consequent slow composition rates. First, it ensured a slow release of nutrients giving a buffering effect to nutrient cycles. Second, the humification of wood residues is thought to contribute disproportionately to the formation of soil organic matter. This has important consequences for the long term productivity of a site since organic matter influences soil structure, water holding capacity, and nutrient storage.

The information summarized above highlights the pivotal role of logs in nutrient cycles and carbon budgets and, in turn, the maintenance of the long-term productivity of forest ecosystems. This role needs to be balanced against the additional removal of nutrients (such as phosphorus) that will take place with the removal of more trees from forest stands (see Crane and Raison 1980) associated with the intensification of harvesting.

ATTRIBUTES OF LOGS AND THEIR ECOLOGICAL ROLES

The attributes of logs, particularly their size and decay status, can influence their ecological values. In Tasmanian Messmate forests, the endangered wood-decaying fungus *Pellinus wahlbergii* is strongly associated with large decayed logs (Zi-Qing Yuan, pers. comm.). The species is virtually absent from other, smaller and less decayed substrates. Pharo and Beattie (2002) found that species richness among bryophtyes living on logs was positively related to the diameter and decay status. Logs in advanced states of decay had the richest bryophyte flora of any substrate in a study in Victorian Mountain Ash forests (Ashton 1986). Ashton (1986) made a detailed study of the bryophytic communities of Mountain Ash forests and found that mosses which form deep mats were best developed on logs within mature and old-growth stands. In another study in Victorian Mountain Ash forests, Lindenmayer *et al.* (1999a) found that moss cover was significantly greater on logs in mature and old stands than those in younger age classes.

The size and decay status of logs is known to be critical for some invertebrates. For example, suitable habitat for the Blind Velvet Worm is characterized by numerous logs that exceed 50 cm in diameter with a soft-rot centre (Mesibov and Ruhberg 1991). Studies of the velvet worm *E. rowelli* have demonstrated the importance of the water content, length and decay status of logs as key habitat attributes for the species (Scott and Rowell 1991; Barclay *et al.* 2000b; Fig. 3). Importantly, the work by Barclay *et al.* (2000b) demonstrated that logs did not become suitable habitat until more than 45 years of decay had occurred.

In contrast to the results obtained for several species of invertebrates, Dickman (1991) believed that some species of ground-dwelling mammals avoided damp and highly decayed rotting logs as shelter sites, possibly because they

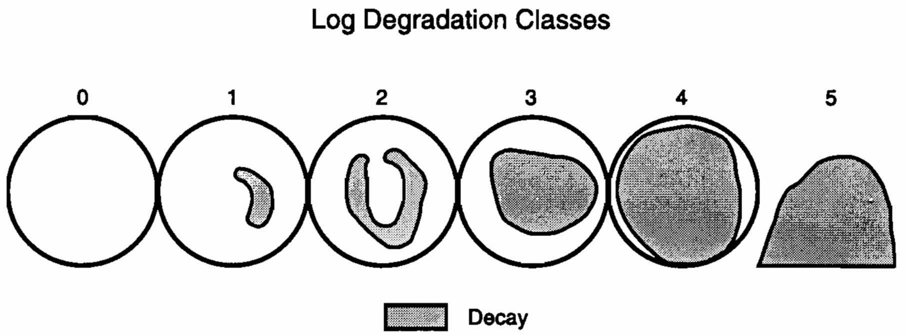

Fig. 3. Decay levels of logs (redrawn from Barclay *et al.* 2000b) and their habitat suitability for the velvet worm *Euperipatoides rowelli*. Logs in the final stages of decay were those most likely to be used by the species.

had poor insulative properties. Large, dry, recently fallen logs appeared to be favoured, particularly those containing cavities with small entrances that precluded potential predators (Dickman 1991). Differences between species in their requirements for logs in different decay states has significant implications for forest management — one of the key topics addressed in the following section.

DISCUSSION

Given the range of ecological roles of logs, it is not surprising that several studies have demonstrated strong habitat associations between log abundance and the occurrence of particular elements of the biota. The Antechinus group of small mammals is perhaps the best documented, with positive relationships quantified for the Agile Antechinus *Antechinus ogilis,* Brown Antechinus, Fawn Antechinus and Yellow-footed Antechinus *A. flavipes* (Barnett *et al.* 1978; Braithwaite 1979; Dickman 1980; Statham and Harden 1982; Friend and Taylor 1985; Mac Nally *et al.* 2001). Another set of well studied examples comes from seminal work on log-animal habitat relationships identified for various species of velvet worms (e.g., Mesibov and Ruhberg 1991; Scott and Rowell 1991; Barclay *et al.* 2000b). However, the cases of the various *Antechinus* spp. and velvet worms are somewhat unusual and most of the ecological roles of logs in Australian forests have received limited study and the majority of relationships are anecdotal without rigorous quantification. Nevertheless, the overview presented above indicates that logs can have many important ecological roles (Lindenmayer and Franklin 1997, 2002).

The impacts of harvesting practices on logs and the potential for stand simplification

The Regional Forest Agreement process in Australia attempted to deliver a land allocation outcome for resolving conflicts over the management and conservation of the nation's native forests. That is, some areas have been gazetted as reserves and the remainder broadly designated for wood and paper production. One problem associated with such a land allocation outcome has been the intensification of harvesting in production forests — a move considered appropriate by some workers (see papers in Connell *et al.* 1997) because of the belief that conservation requirements will be dealt with adequately in the reserve system. However, the importance of off-reserve forests for biodiversity conservation is well known (Recher 1996; Hale and Lamb 1997; Lindenmayer and Franklin 1999) and a shift toward the intensification of harvesting outside the reserve system is likely to have negative impacts on a range of ecological values (Lindenmayer and Franklin 2002). While conservation strategies within wood production forests like the reservation of patches of old growth forest and the establishment of wildlife corridors are undoubtedly important, it is critical to ensure that stand-level approaches to biodiversity conservation are also implemented (reviewed by Lindenmayer and Franklin 2002). Failure to take account of the need for the maintenance and long-term recruitment of logs in native forests subject to recurrent harvesting will ultimately lead to the simplification of stand structure — with a range of potentially negative outcomes. Indeed, stand simplification has been recognized as a major problem for the conservation of biodiversity and the maintenance of ecological processes in managed forests all over the world (Franklin *et al.* 1997; Linder and Ostlund 1998), and in some places such as Germany for more than 100 years (Gayer 1886). Stand simplification effects will be most prominent in logging coupes subject to recurrent harvesting (i.e., cutting over several rotations) (Meggs 1997). For example, Barclay *et al.* (2000b) forecast negative impacts on the abundance of decayed logs and associated biodiversity (e.g., velvet worms) resulting from the transition from past selective harvesting to more intensive cutting regimes that integrate both sawlog removal and woodchipping in the forests of southeastern New South Wales.

A key problem for biodiversity conservation in parts of wood production forests subject to recurrent intensive harvesting is that many taxa rely on old large diameter logs in a highly decayed state (including those that contain cavities) (see Williams and Faunt 1997; Barclay *et al.* 2000b). Such types of logs can take a prolonged period to develop and failure to make adequate provision for their perpetual supply in logging coupes may have significant negative impacts on the taxa known to be directly or indirectly dependent on them (Recher 1996). For example, Lunney *et al.* (1991) predicted a decline of the skink *Eulamprus heatwolei* in Mumbulla State Forest in south-eastern Australia, due to the decline of large logs — an essential habitat component for the species. Suitably large logs were not projected to be produced by the size classes of trees present during the 40 year commercial rotation age in this area.

Large-diameter living and dead standing trees are important sources of stems that are eventually recruited to the forest floor as logs (Harmon *et al.* 1986). However, the frequency and intensity of repeated harvesting events in wood production forests will limit the development of large diameter standing trees (Gibbons and Lindenmayer 2002) and Smith *et al.* (1992) predicted that:-

> *"The resource most susceptible to long term reduction [in wood production forests] is large log cover, which results from the natural collapse and decay of old growth stems. This problem is likely to be most severe in high quality hardwood forests where harvesting intensity is high and only a small portion of forest stems are able to senesce naturally."*

Notably, in studies of production forests in western North America, Spies *et al.* (1988) concluded that large logs were the structural elements slowest to recover following human disturbance. The retention of trees at the time of harvesting may partially alleviate this problem. Indeed, Grove (2002) noted that tree retention in Australian production forests was essential to avoid repeating the extinctions of many dead-wood dependent invertebrates that had occurred in the Northern Hemisphere. However, the limited current rate of tree retention in many areas of the Australian wood production estate (Gibbons and Lindenmayer 1997, 2002) means that existing retained trees are likely to contribute only a small fraction of the stems that would be recruited to the forest floor in unharvested forests. This indicates a need to increase the number of retained trees on logged sites. Mortality among a subset of the retained trees before they attain large sizes further increases the number of stems on logged sites need to be exempt from cutting (Ball *et al.* 1999). In addition, some stems will need to grow through and remain standing over several cutting events and/or rotations to ensure the dimensions of logs are the size required by particular elements of the biota. Assessments of the long-term requirements for the numbers and types of logs in different states of decay needed within harvested areas might be facilitated by the use of modelling tools such as those used for such purposes in North America (Sturvenant *et al.* 1979). Such approaches have been applied in modelling the dynamics of trees with hollows in wood production forests (e.g., Ball *et al.* 1999; Gibbons 1999) and they could be adapted to simulate log resources in these same forests.

Careful ecological consideration needs to be given to the numbers of retained logs required to maintain key elements of biodiversity. This is because relationships between the occurrence of fauna and log abundance may not be linear. For example, Mac Nally *et al.* (2002) found that when log volumes exceeded 40–45 tonnes/ha, population densities of the Brown Treecreeper increased significantly. The Yellow-footed Antechinus also appeared to respond positively to similar log volumes in the same ecosystem (Mac Nally *et al.* 2002).

Another key consideration for the maintenance of logs in managed forests is the difference in habitat preferences between different groups (e.g., small mammals versus invertebrates; see above). This highlights the need to maintain logs in different size classes and states of decay within managed forests — a requirement that also has significant implications for the overall number of trees that need to be retained and the time over which new trees need to be recruited to the forest floor. Hence, changes to the abundance of large standing trees resulting from logging operations (Gibbons and Lindenmayer 2002) and, in turn, the abundance of logs, are potentially important changes to stand structural complexity, particularly after several rotations (Meggs 1997). However, in comparison with forests elsewhere in the world, there have been remarkably few studies of logs in Australian temperate forest ecosystems. In view of this major knowledge gap, we suggest there is an urgent need to compare the abundance and characteristics of logs in managed and unmanaged eucalypt forests (see Meggs 1996) and to determine whether such differences have implications for the conservation of biodiversity. Such research is critical given that the intensification of forestry represents essentially new forms of harvesting in Australia of which the impacts are poorly understood.

Potential impacts of forestry operations on other factors

In addition to the retention of adequate numbers of standing trees to promote log recruitment, the potential impacts of other forestry practices need to be taken into account. Three major ones are (1) the impacts of mechanical damage created by harvesting machinery on logs and on soil conditions during harvesting, (2) the impacts on logs of high-intensity regeneration fires used to promote the regeneration of harvested sites, and, (3) the impacts of recurrent prescribed burning on logs and fauna and flora associated with such habitats.

Logs may be broken up by harvesting machinery. Such damage may be important because of the time required for logs to decay to stages where they are suitable habitat for particular species (e.g., some types of velvet worms; see Barclay *et al.* 2000b) and thus the need to ensure that some logs persist through several rotations on logged sites — the concept of ecological continuity discussed below. The potential for damage to log resources is real given the known impacts on other entities such as soil conditions through compaction by harvesting machinery (e.g., Rab 1998). Indeed, the harvesting of residual trees and "waste wood" is likely to result in greater soil compaction and disturbance than sawlog-only cutting — impacts from which forest ecosystems may take up to 100 years to recover (Rab 1992). The effects of high-intensity regeneration burns on log and associated species are also poorly understood (Taylor 1990). However, a number of species of log-dependent invertebrates are thought to take a prolonged period to recolonize sites subject to high intensity regeneration fires (Forestry Practices Board 1998).

The impacts of prescribed burning on elements of forest structure such as logs is a controversial area of forest management and the results of the array of studies completed to date are equivocal (reviewed by Williams and Gill 1995; Gill *et al.* 1999). King (1985) studied litter invertebrates and their small mammal predators. He found log cover was reduced by prescribed burning and concluded there could be a cumulative impact whereby these structural components of forests could become limiting for some species. Similarly, State Forests of NSW (1996) noted the accelerated decay of large logs as one of the impacts of frequent low intensity prescribed fires. Smith *et al.* (1992) found that many vertebrate taxa were negatively associated with frequently burned forests and logs were among the important habitat attributes reduced under this management regime. In one of the longest running studies completed to date, York (1996 in Gill *et al.* 1999) showed how log attributes changed with prescribed burning such as the extent of charring and desiccation of the outer log surface. There also was a large shift in the composition of invertebrate communities with a trend toward species more tolerant of drier and more open forest environments. Hannah *et al.* (1998) also found that log were less common in forests subject to recurrent prescribed burning and they speculated about the negative impacts of such changes on groups closely associated with such structure such as reptiles.

The three aspects of forest management outlined above clearly require consideration as part of the development of harvesting prescriptions. The impacts of the first two, in particular, must also be key topics for future research in production forests.

Prescriptions to better manage logs in wood production forests

Few forest management agencies in Australia have detailed prescriptions to guide the retention of logs and their long-term recruitment within harvested areas. This is despite the fact that:- (1) some organisations are aware that recurrent timber harvesting will reduce log numbers in managed stands (State Forests of NSW 1995), (2) the loss of large hollow logs is listed as a key process threatening species like the Spotted-tailed Quoll *Dasyurus maculatus* in states such as New South Wales (New South Wales National Parks and Wildlife Service 1999), and, (3) the need for the management of logs is recognized in the Draft Australian Forestry Standard (Australian Forestry Standard Steering Committee and Technical reference Committee 2001). The current limited range of prescriptions is a major deficiency given the array of critical ecological roles played by logs and the known relationships between elements of biodiversity and log attributes (e.g., Hannah *et al.* 1998; Barclay *et al.* 2000b). In Tasmania, the Forestry Practices Board (1998) has made recommendations for the management of logs for a range of threatened invertebrates. These include:- (1) setting aside Wildlife Priority Areas (Taylor 1991), (2) the retention of rotting logs (particularly within wildlife habitat tree clumps) within harvested sites, (3) the exclusion of high-intensity regeneration burns in nominated areas, and, (4) limitations on the conversion of native forest to plantations in areas supporting suitable habitat for particular taxa. One of the terms of licensing for timber harvesting in southern New South Wales where is that firewood harvesting must not occur in harvested compartments where threatened log-using species such as the Spotted-tailed Quoll and the Bush Stone-Curlew *Burhinus grallarius* have been recorded (Resource and Conservation Assessment Council 2002). In the Jarrah forests of south-west Western Australia, current prescriptions are for the retention of one hollow log or stump per hectare even if it shows no obvious signs of animal use, as well as all logs longer than three metres and a hollow pipe more than 10 cm in diameter (Department of Conservation and Land Management 1995).

In contrast to the general lack of prescriptions for the management of logs in Australian forests, there are many overseas examples where their values are taken into account as part of on-site harvesting prescriptions (e.g., Brown 1985; Forest Ecosystem Assessment Management Team 1993). For example, a study in the United States of America by Graham *et al.* (1994) discussed the quantities of logs needed to be retained per hectare of logged forest to maintain forest productivity. In the Pacific Northwest of the United States of America, Harmon (2001b) noted that forest managers are moving away from the extensive removal of "woody debris" and adopting prescriptions to maintain and even increase it in managed stands. In Scandinavia log retention within harvested forests is known to facilitate the persistence of diverse groups of fungi that might otherwise be lost from timber-production landscapes (Niemelä *et al.* 1995; Sverdrup-Tygeson and Lindenmayer 2002). Logs left in these environments are also used by saproxylic beetles (Niemelä *et al.* 1993, 1995;

Kaila *et al.* 1997). In parts of northwestern North America, retaining selected structures as part of a harvesting operation can provide the resources required by non-autotrophic organisms such as mycorrhizal fungi that inoculate the remainder of the harvested area and facilitate stand regeneration (Perry 1994; Simard *et al.* 1997).

Prescriptions to maintain spatial and temporal continuity in the availability of logs

In addition to the quantity and decay status of logs that need to be retained in harvested forests, it also will be important to examine spatial patterns of logs. This is because of the importance of logs for animal movement (including dispersal) (see above) and, in turn, the potential to fragment populations of species by disrupting the natural spatial continuity (MacEachern 2001). The long-term availability or temporal continuity of logs is also a significant issue and one that warrants consideration in formulating prescriptions. Continuity in the availability of logs could be critical for the persistence of taxa with limited mobility and which are slow to recolonize harvested areas. Indeed, this issue has been well recognized in Scandinavian forests where the concept of temporal continuity of logs (termed ecological continuity) has been developed (Angelstam and Pettersson 1997). Ecological continuity has been defined as:-

> *"an ecological attribute that is maintained within an area over time" [Gundersen and Rolstad 1998].*

In Nordic countries, the continuous availability of logs is believed to have strongly influenced the occurrence of an array of red-listed invertebrates and fungi associated with wood-decaying habitats (e.g., Høiland 1996; Økland 1996; Lindblad 1998; Svendrup-Thyeson 2001), Provision for the continuous presence of large rotting logs in managed stands is now recognized as a critical part of ecologically sustainable forest management in those nations. Logging practices in many parts of Australia need to follow the lead of other countries and make provision for spatial and temporal continuity in the provision of logs in managed forests.

CONCLUSIONS

Proponents of the intensification of harvesting practices and large scale industrial forestry projects in Australian native forests (e.g., Connell *et al.* 1999; Leech 2001) have often overlooked some of the fundamental structural attributes and ecological processes that are essential to the functioning of forest ecosystems. Advocates of these projects argue that removing "residual wood" is "cleaning up the forest" and "value-adding" (Leech 2001). However, from a forest ecology perspective, efforts to remove large quantities of defective stems and logs will be "value-subtracting" for some elements of the biota and some key ecological processes. Notably, a major recent review on maintaining the habitat value of managed forests emphasized the importance for biodiversity of leaving so-called logging "waste" in the forest rather than removing or burning it (Grove 2001b). This recommendation is entirely congruent with recent empirical studies which have demonstrated the value of leaving timber to rot on the forest floor (Bonham *et al.* 2002).

Perhaps part of the problem lies with a lack of understanding of the importance of key structural features of natural forests such as logs. In future, forest ecologists may be better to adopt new terminology that better encapsulates the roles of logs and defective stems. Terms such as rotting logs, coarse woody debris and waste wood might be replaced by log habitat, nursery logs, foraging and moisture oases, and nutrient cycling buffers. While it is unlikely that such terminology will be widely adopted, in the face of activities like the proposed intensification of harvesting, it will be critical for forest ecologists to better communicate:- (1) the importance of key structural attributes for forest biodiversity and ecosystem function, and (2) that converting native forests outside the reserve system to "de facto plantations" is bad conservation biology and poor natural resource management.

ACKNOWLEDGEMENTS

David Lindenmayer would like to thank a range of colleagues with whom various collaborative studies made this review possible — Ann Svendrup-Thyeson, Ross Cunningham, Ryan Incoll, Chris MacGregor and Jerry Franklin. James Trappe provided unpublished data on a range of fungi that are associated with logs. We are most grateful to Brendan Mackey and his students for discussions on the role of logs in the carbon cycle. Rosie Smith and Monica Ruibal assisted with the collection of literature. Additional papers for this project were provided by Alistair Robertson, Dave Rowell, Emma Pharo and Simon Grove. Comments by Harry Recher and three anonymous referees greatly improved earlier versions of this manuscript. DBL would *not* like to thank the proponents of large scale biomass burning power stations, charcoal plants and the intensification of forest harvesting who made this review necessary.

REFERENCES

Amaranthus, M., Trappe, J. M., Bednar, L. and Arthur, D., 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. *Can. J. For. Res.* **24:** 2157–165.

Andrew, N., Rodgerson, L. and York, A., 2000. Frequent fuel-reduction burning: the role of logs and associated leaf litter in the conservation of ant biodiversity. *Aust. Ecol.* **25:** 99–107.

Angelstam, P., 1996. The ghost of forest past — natural disturbance regimes as a basis for reconstruction for biologically diverse forests in Europe. Pp. 287–337 *in* Conservation of Faunal Diversity in Forested Landscapes ed by R. M. DeGraaf and R. I. Miller. Chapman and Hall, London.

Angelstam, P. and Pettersson, B., 1997. Principles of present Swedish forest biodiversity management. *Ecol. Bull.* **46:** 191–203.

Ashton, D. H., 1976. The development of even-aged stands of *Eucalyptus regnans* F. Muell. in Central Victoria. *Aust. J. Bot.* **24:** 397–414.

Ashton, D. H., 1986. Ecology of bryophytic communities in mature *Eucalyptus regnans* F. Muell. forest at Wallaby Creek, Victoria. *Aust. J. Bot.* **34:** 107–29.

Attiwill, P. M. and Leeper, G. W., 1987. Forest Soils and Nutrient Cycles. Melbourne University Press, Melbourne.

Australian Forestry Standard Steering Committee and Technical Reference Committee, 2001. Draft Australian Forestry Standard. Australian Forestry Standard Steering Committee and Technical Reference Committee, Canberra. August 2001.

Bader, P., Jansson, S. and Johnson, B. G., 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. *Biol. Cons.* **72:** 355–62.

Ball, I., Lindenmayer, D. B. and Possingham, H. P., 1999. A tree hollow dynamics simulation model. *For. Ecol. Man.* **123:** 179–94.

Barclay, S. D., Rowell, D. M. and Ash, J. E., 2000a. Pheromonally-mediated colonization patterns in the Velvet Worm *Euperipatodies rowelli* (Onycophora: Peripatopsidae). *J. Zool.* **250:** 437–46.

Barclay, S. D., Ash, J. E. and Rowell, D. M., 2000b. Environmental factors influencing the presence and abundance of a log-dwelling invertebrate *Euperipatodies rowelli* (Onychophora: Peripatopsidae). *J. Zool.* **250:** 425–36.

Barker, J., Grigg, G. C. and Tyler, M. J., 1995. A Field Guide to Australian Frogs. Surrey Beatty & Sons, Chipping Norton.

Barker, P. and Kirkpatrick, J. B., 1994. *Phyllocladus aspleniifolius*: variability in the population structure, the regeneration niche and dispersion patterns in Tasmanian forest. *Aust. J. Bot.* **42:** 163–90.

Barnett, J. L., How, R. A. and Humphreys, W. F., 1978. The use of habitat components by small mammals in eastern Australia. *Aust. J. Ecol.* **3:** 277–85.

Bauhaus, J., 1999. Silvicultural practices in Australian native forests — an introduction. *Aust. For.* **62:** 217–22.

Bennett, R., 1997. Reptiles and frogs of the Australian Capital Territory. National Parks Association of the ACT Inc, Canberra, ACT.

Berg, A., Ehnstrom, B., Gustaffson, L., Hallingback, T., Jonsell, M. and Weslien, J., 1994. Threatened plant, animal and fungus species in Swedish forests: distribution and habitat associations. *Cons. Biol.* **8:** 718–31.

Beruldsen, G., 1980. A Field Guide to Nests and Eggs of Australian Birds. Rigby, Adelaide

Beschta, R. L. and Platts, W. S., 1986. Morphological features of small streams: significance and function. *Water Res. Bull.* **22:** 369–79.

Bobiec, A., 2002. Living stands and dead wood in the Białowieża forest: suggestions for restoration management. *For. Ecol. Man.* **165:** 125–40.

Bonham, K. J., Mesibov, R. and Bashford, R., 2002. Diversity and abundance of some ground-dwelling invertebrates in plantation vs. native forests in Tasmania, Australia. *For. Ecol. Man.* **158:** 237–47.

Bougher, N. L. and Syme, K., 1998. Fungi of Southern Australia. University of Western Australia Press, Perth.

Braithwaite, R. W., 1979. Social dominance and habitat utilisation in *Antechinus stuartii* (Marsupialia). *Aust. J. Zool.* **27:** 517–28.

Brown, E. R. (ed), 1985. Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington. Part 1 — Chapter narratives. USDA Forest Service. PNW-R6-F&WL-192. Portland, Oregon. June 1985.

Brown, G. W. and Nelson, J. L., 1993. Influence of successional stage of *Eucalyptus regnans* (Mountain Ash) on habitat use by reptiles in the Central Highlands of Victoria. *Aust. J. Ecol.* **18:** 405–18.

Brown, G. W. and Nicholls, A. O., 1994 Comparative census techniques and modelling of habitat utilisation by reptiles in northern Victoria. Pp. 283–90 *in* Herpetology in Australia: a Diverse Discipline ed by D. Lunney and D. Ayers. Surrey Beatty & Sons, Chipping Norton, New South Wales.

Brown, S., Jiangming, M., McPherson, J. K. and Bell, D. T., 1996. Decomposition of woody debris in Western Australian forests. *Can. J. For. Res.* **26:** 954–66.

Bunnell, F. L., Kremsater, L. L. and Wind, E., 1999. Managing to sustain vertebrate richness in forests of the Pacific Northwest: relationships within stands. *Environ. Rev.* **7:** 97–146.

Calaby, J., 1995. Fawn Antechinus. Pp. 42 *in* Complete Book of Australian Mammals ed by R. Strahan. Cornstalk Publishing, Singapore.

Campbell, A. J. and Tanton, M. T., 1981. Effects of fire on the invertebrate fauna of soil and litter of a eucalypt forest. Pp. 215–41 *in* Fire and the Australian Biota ed by A. M. Gill, R. H. Groves and I. R. Noble. Australian Academy of Science, Canberra.

Catling, P. C. and Burt, R. J., 1995. Studies of the ground-dwelling mammals of the eucalypt forests in south-eastern New South Wales — the effect of habitat variables on distribution and abundance. *Wildl. Res.* **22:** 271–88.

Christensen, P., 1975. The breeding burrow of the Banded Ant-eater or Numbat (*Myrmecobius fasciatus*). *West. Aust. Nat.* **13:** 32–34.

Christensen, P., Recher, H. and Hoare, J., 1981. Responses of Open forest to Fire Regimes Pp. 367–94 *in* Fire and the Australian Biota ed by A. M. Gill, R. H. Groves and I. R. Noble. Australian Academy of Science, Canberra.

Christensen, P., Maisey, K. and Perry, D. H., 1984. Radio-tracking the Numbat, *Myrmecobius fasciatus*, in the Perup Forest of Western Australia. *Aust. Wildl. Res.* **11:** 275–88.

Claridge, A. W. and Lindenmayer, D. B., 1993. The Mountain Brushtail Possum, *Trichosurus caninus* Ogilby: a disseminator of fungi in the Mountain Ash forests of the Central Highlands of Victoria? *Vic. Nat.* **110:** 91–95.

Claridge, A. W. and May, T. W., 1994. Mycophagy among Australian mammals. *Aust. J. Ecol.* **19:** 251–75.

Claridge, A. C. and Lindenmayer, D. B., 1998. Consumption of hypogeous fungi by the Mountain Brushtail Possum (*Trichosurus caninus*) in eastern Australia. *Mycol. Res.* **102:** 269–72.

Claridge, A. W., Barry, S. C., Cork, S. J. and Trappe, J. M., 2000a. Diversity and habitat relationships of hypogeous fungi. II. Factors influencing the occurrence and number of taxa. *Biodiver. Cons.* **9:** 175–99.

Claridge, A. W., Cork, S. J. and Trappe, J. M., 2000b. Diversity and habitat relationships of hypogeous fungi. I. Study design, sampling techniques and general survey results. *Biodiver. Cons.* **9:** 151–73.

Cogger, H., 2000. Reptiles and Amphibians of Australia. Revised Edition. Reed, Sydney, Australia.

Connell, M. J., Raison, R. J. and Brown, A. G. (eds), 1999. Intensive Management of Regrowth Forest for Wood Production in Australia. Proceedings of the National Workshop 18–20 May 1999, Orbost, Victoria, Australia. CSIRO Publishing, Melbourne.

Crane, W. J. and Raison, R. J., 1980. Removal of phosphorus in logs when harvesting *Eucalyptus delegatensis* and *Pinus radiata* forests on short and long rotations. *Aust. For.* **43:** 253–60.

Crook, D. and Robertson, A., 1999. Relationships between riverine fish and woody debris: implications for lowland rivers. *Marine Freshwater Res.* **50:** 941–53.

Cullen, P. J., 1987. Regeneration patterns in populations of *Arthrotaxis selaginoides* D. Don from Tasmania. *J. Biogeo.* **14:** 39–51.

Curry, G. N., 1991. The influence of proximity to plantation of diversity and abundance of bird species in an exotic pine plantation in north-eastern New South Wales. *Wildl. Res.* **18:** 299–314.

Davey, S. M., 1989. The environmental relationships of arboreal marsupials in a eucalypt forest: a basis for Australian wildlife management. PhD thesis. Dept. Forestry, The Australian National University, Canberra.

Department of Conservation and Land Management, 1995. Silvicultural guidelines 1/95: silvicultural practice in Jarrah Forest. Department of Conservation and Land Management, Perth, Western Australia.

Dickman, C. R., 1980. Ecological studies of *Antechinus stuartii* and *Antechinus flavipes* (Marsupialia: Dasyuridae) in open-forest and woodland habitats. *Aust. Zool.* **20:** 433–46.

Dickman, C. R., 1991. Use of trees by ground-dwelling mammals: implications for management. Pp. 125–36 *in* Conservation of Australia's Forest Fauna ed by D. Lunney. Royal Society of N.S.W., Sydney.

Ehmann, H., 1992. Encyclopedia of Australian Reptiles. Angus and Robertson, Sydney.

Environmental Resources Management Australia, 2001. Environmental Impact Statement. Wood processing and metallurgical carbon facility for Australian Silicon Operations Pty Ltd. Environmental Resources Management Australia, November 2001.

Forest Ecosystem Management Assessment Team, 1993. Forest ecosystem management: an ecological, economic, and social assessment. Various pagination. USDA Forest Service, Portland, Oregon. Various pagination.

Forest Practices Board, 1998. Threatened Fauna Manual for Production Forests in Tasmania. Forest Practices Board, Hobart, Tasmania.

Franklin, J. F., Shugart, H. H. and Harmon, M. E., 1987. Tree death as an ecological process: the causes, consequences, and variability of tree mortality. *Bioscience* **37:** 550–56.

Franklin, J. F., Lindenmayer, D. B., MacMahon, J. A., McKee, A., Magnusson, J., Perry, D. A., Waide, R. and Foster, D. R., 2000. Threads of continuity: ecosystem disturbances, biological legacies and ecosystem recovery. *Cons. Biol. Prac.* **1:** 8–16.

Friend, G. R., 1982. Mammal populations in exotic pine plantations and indigenous eucalypt forests in Gippsland, Victoria. *Aust. For.* **45:** 3–18.

Friend, J. A., 1990. Myrmecobiidae. Pp. 583–90 *in* Fauna of Australia. Volume 1B. Mammalia ed by D. W. Walton and B. J. Richardson. Australian Government Printing Service, Canberra.

Gay, F. J. and Calaby, J. H., 1970. Termites of the Australian region. Pp. 393–448 *in* Biology of Termites ed by K. Krishna and F. M. Weesner. Academic Press, New York.

Gayer, K., 1886. Der gemischte Wald — seine Begründung and Pflege, insbesondere durch Horst- und Gruppenwirtschaft. Verlag Paul Parey, Berlin.

Gibbons, P., 1999. Habitat tree retention in wood production forests. Ph.D thesis. The Australian National University, Canberra.

Gibbons, P. and Lindenmayer, D. B., 1997. Developing tree retention strategies for hollow-dependent arboreal marsupials in eucalypt forests managed for timber production. *Aust. For.* **60:** 29–45.

Gibbons, P. and Lindenmayer, D. B., 2002. Tree Hollows and Wildlife Conservation in Australia. CSIRO Publishing, Melbourne.

Gill, A. M., Woinarski, J. C. and York, A., 1999. Australia's biodiversity — responses to fire. Plants, birds and invertebrates. Environment Australia Biodiversity Technical Paper **1:** 1–266.

Gippel, C. J., 1995. Environmental hydraulics of large woody debris in streams and rivers. *J. Environ. Engin.* **121:** 388–95.

Gippel, C. J., Finlayson, B. L. and O'Neill, I. C., 1996. Disturbance and hydraulic significance of large woody debris in a lowland Australian river. *Hydrobiol.* **318:** 179–94.

Godsell, J., 2000. Eastern Quoll. Pp. 70–71 *in* The Mammals of Australia ed by R. Strahan. Reed, New Holland, Sydney.

Goldingay, R., Daly, G. and Lemckert, F., 1996. Assessing the impacts of logging on reptiles and frogs in the montane forests of southern New South Wales. *Wildl. Res.* **23:** 495–510.

Greenslade, P., 1985. Conservation Priorities in Tasmanian Non-marine Invertebrates. Unpublished report. Tasmanian National Parks and Wildlife Service, Hobart.

Greenslade, P., 1990. Collembola. Pp. 252–64 *in* The Insects of Australia. Volume 1. Second Edition. Melbourne University Press, Melbourne.

Grove, S. J., 2001a. Extent and decomposition of dead wood in Australian lowland tropical rainforest with different management histories. *For. Ecol. Man.* **154:** 35–53.

Grove, S. J., 2001b. Developing appropriate mechanisms for sustaining mature timber habitat in managed natural forest stands. *Internat. For. Review* **3:** 272–83.

Grove, S. J., 2002. The influence of forest management history on the integrity of sparoxylic beetle fauna in an Australian lowland tropical rainforest. *Biol. Cons.* **104:** 149–71.

Gundersen, V. and Rolstad, J., 1998. Nøkkelbiotoper i skog. En vurdering av nøkkelbiotoper som forvaltningstiltak for bevaring av biologisk mangfold i skog. NISK, Ås.

Hale, P. and Lamb, D. (eds), 1997. Conservation Outside Reserves. Centre for Conservation Biology, University of Queensland, Brisbane.

Halstead-Smith, J., 1999. The use of coarse woody debris by ground-dwelling small mammals. BSc (Hons) thesis. Monash University, Melbourne.

Hannah, D. S., Smith, G. C. and Agnew, G., 1998. Reptile and amphibian composition in prescribed burnt dry sclerophyll forest, southern Queensland. *Aust. For.* **61:** 34–39.

Harmon, M. E., 2001a. Carbon sequestration in forests. Addressing the scale question. *J. For.* **99:** 24–29.

Harmon, M. E., 2001b. Moving toward a new paradigm for woody detritus management. *Ecol. Bull.* **49:** 269–78.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Kromack Jnr, K. and Cummins, K. W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances Ecol. Res.* **15:** 133–302.

Harmon, M. E., Ferrell, W. K. and Franklin, J. F., 1990. Effects of carbon storage on conversion of old-growth forest to young forests. *Science* **9:** 699.

Heatwole, H. F. and Taylor, J., 1987. Ecology of Reptiles. Surrey Beatty & Sons, Chipping Norton, Sydney.

Higgins, P. J., Peter, J. M. and Steele, W. K. (eds), 2001. Handbook of Australian, New Zealand and Antarctic Birds, Volume 5, Tyrant-flycatchers to Chats. Oxford University Press, Melbourne.

HØiland, K. and Bendiksen, E., 1996. Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sor-Trondelag County, Central Norway. *Nordic J. Bot.* **16:** 643–59.

Howard, T. M., 1973. Studies in the ecology of *Nothofagus cunninghamii* Oerst. I. Natural regeneration on the Mt. Donna Buang massif, Victoria. *Aust. J. Bot.* **21:** 67–78.

Hunter, M. L., 1990. Wildlife, Forests and Forestry. Principles for Managing Forests for Biological Diversity. Prentice Hall, Englewood Cliffs.

Jacobs, M. R., 1955. Growth Habits of the Eucalypts. Forestry and Timber Bureau. Australian Government Printing Office, Canberra, Australia.

Jarman, S. J. and Fuhrer, B., 1995. Mosses and Liverworts of Rainforest in Tasmania. CSIRO Publications (Melbourne) and Forestry Tasmania (Hobart).

Kaila, L., Martikainen, P. and Puntilla, P., 1997 Dead trees left in clearcuts benefit Coleoptera adapted to natural disturbances in boreal forests. *Biodiv. Cons.* **6:** 1–8.

Kanowski, P. and Buchy, M., 1999. Pp. 78–84 *in* Intensive Management of Regrowth Forest for Wood Production in Australia ed by M. J. Connell, R. J. Raison and A. G. Brown. Proceedings of the National Workshop 18–20 May 1999, Orbost, Victoria, Australia. CSIRO Publishing, Melbourne, Australia.

King, G. C., 1985. The effect of fire on small mammal fauna and their resources in two forest types. Thesis for Master of Natural Resources, University of New England, Armidale.

Kirkpatrick, J. B., 1997. Vascular plant-eucalypt interactions. Pp. 227–45 *in* Eucalypt Ecology ed by J. E. Williams and J. C. Woinarski. Cambridge University Press, Cambridge.

Koehn, J., 1993. Fish need trees. *Vic. Nat.* **110:** 255–57.

Krankina, O. N., Harmon, M. E. and Griazkin, A. V., 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modelling potential implications at the stand level. *Can. J. For. Res.* **29:** 1–20.

Kutt, A. S., 1994. Initial observations on the effect of thinning eucalypt regrowth on heliothermic skinks in lowland forests, East Gippsland Victoria. Pp. 187–96 *in* Herpetology in Australia: a Diverse Discipline ed by D. Lunney and D. Ayers. Surrey Beatty & Sons, Chipping Norton, Sydney.

Lamb, D., 1991. Variability and change in nutrient cycling in Australian rainforests. Pp. 83–103 *in* The Rainforest Legacy, Australian National Rainforests Study Vol. 2 — Flora and Fauna of the Rainforests ed by G. Werren and P. Kershaw. Australian Government Publishing Service, Canberra.

Laven, N. and Mac Nally, R., 1998. Association of birds with coarse woody debris in box-ironbark forests of central Victoria. *Corella* **22:** 56–60.

Lee, P. C., Crites, S., Nietfeld, M., Van Nygen, H. and Stelfox, J. B., 1997. Characteristics and origins of deadwood material in Aspen-dominated boreal forests. *Ecol. Appli.* **7:** 691–701.

Leech, J. W., 2001. Consultancy to Review of State Forests Capacity to Supply Residue Wood from the South Coast Region. Forestry Systems. April 2001.

Lewis, J. G., 1981. The Biology of Centipedes. Cambridge University Press, Cambridge.

Lill, A., 1996. Foraging behavioural ecology of the Superb Lyrebird. *Corella* **20:** 77–87.

Lindblad, I., 1998. Wood-inhabiting fungi on fallen logs of Norway spruce: Relations to forest management and substrate quality. *Nordic J. Bot.* **18:** 243–55.

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T. and Smith, A. P., 1990a. The conservation of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia. II. The loss of trees with hollows and its implications for the conservation of Leadbeater's Possum *Gymnobelideus leadbeateri* McCoy (Marsupialia: Petauridae). *Biol. Cons.* **54:** 133–45.

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T. and Smith, A. P., 1990b. The conservation of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia. I. Factors effecting the occupancy of trees with hollows. *Biol. Cons.* **54:** 111–31.

Lindenmayer, D. B., Cunningham, R. B. and Donnelly, C. F., 1997. Decay and collapse of trees with hollows in eastern Australian forests: impacts on arboreal marsupials. *Ecol. Appl.* **7:** 625–41.

Lindenmayer, D. B. and Franklin, J. F., 1997. Forest structure and sustainable temperate forestry: A case study from Australia. *Cons. Biol.* **11:** 1053–068.

Lindenmayer, D. B. and Recher, H. F., 1998. Aspects of ecologically sustainable forestry in temperate eucalypt forests – beyond an expanded reserve system. *Pac. Cons. Biol.* **4:** 4–10.

Lindenmayer, D. B., Lacy, R. C. and Viggers, K. L., 1998. Modelling survival and capture probabilities of the Mountain Brushtail Possum (*Trichosurus caninus*) in the forests of south-eastern Australia using trap-recapture data. *J. Zool.* **245:** 1–13.

Lindenmayer, D. B., Incoll, R. D., Cunningham, R. B. and Donnelly, C. F., 1999a. Attributes of logs in the Mountain Ash forests in south-eastern Australia. *For. Ecol. Man.* **123:** 195–203.

Lindenmayer, D. B., Cunningham, R. B., Pope, M. L. and Donnelly, C. F., 1999b. A field-based experiment to examine the response of mammals to landscape context and habitat fragmentation. *Biol. Cons.* **88:** 387–403.

Lindenmayer, D. B. and Franklin, J. F., 1999. Managing unreserved forest for biodiversity conservation: The importance of matrix. Pp. 13–25 *in* Nature Conservation in Production Environments: Managing the Matrix ed by J. Craig, N. Mitchell and D. A. Saunders. Surrey Beatty & Sons, Sydney.

Lindenmayer, D. B., Cunningham, R. B. and Donnelly, C. F., 2000. Structural features of Australian old growth montane ash forests. *For. Ecol. Man.* **134:** 189–204.

Lindenmayer, D. B. and Franklin, J. F., 2002. Conserving Forest Biodiversity: a Comprehensive Multi-scaled Approach. Island Press, Washington, D.C.

Linder, P. and Östlund, L., 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. *Biol. Cons.* **85:** 9–19.

Lovett, S. and Price, P. (eds), 1999. Riparian Land Management Technical Guidelines. Volume 1: Principles of Sound Management. Land and Water Resources Research and Development Corporation, Canberra.

Luke, R. H and McArthur, A. G., 1978. Bushfires in Australia. Australian Government Publishing Service, Canberra.

Lunney, D., Eby, P. and O'Connell, M., 1991. Effects of logging, fire and drought on three species of lizards in Mumbulla State Forest on the south coast of New South Wales. *Aus. J. Ecol.* **16:** 33–46.

MacArthur, R. H., Recher, H. F. and Cody, M. L., 1966. On the relation between habitat selection and species diversity. *Amer. Nat.* **100:** 319–22.

MacEachern, S., 2001. The consequences of habitat fragmentation on the wood-dwelling cockraoch *Panesthia australis* (Blattaria, Blaberidae Panesthiinae). BSc. Hons thesis. La Trobe University, Melbourne.

McKenny, H. J. and Kirkpatrick, J. B., 1999. The role of fallen logs in the regeneration of tree species in Tasmanian mixed forest. *Aust. J. Bot.* **47:** 745–53.

Mackensen, J. and Bauhus, J., 1999. The decay of coarse woody debris. National Carbon Accounting System. Technical Report No. 6. Australian Greenhouse Office. Commonwealth of Australia, November 1999.

Mac Nally, R., Parkinson, A., Horrocks, G., Conole, L. and Tzaros, C., 2001. Relationships between terrestrial vertebrate diversity, abundance and availability of coarse woody debris on south-eastern Australian floodplains. *Biol. Cons.* **99:** 191–205.

Mac Nally, R., Horrocks, G. and Pettifer, L., 2002. Experimental evidence for potential beneficial effects of fallen timber in forests and implications for habitat restoration. *Ecol. Appl.* (in press).

Martin, P. H., Nabuurs, G., Aubinet, M., Karjalainen, T., Vine, E., Kinsman, J. and Heath, L., 2001. Carbon sinks in temperate forests. *Ann. Rev. Energy Environ.* **26:** 435–65.

Maser, C. and Trappe, J. M., 1984. The Seen and Unseen World of the Fallen Tree. U.S.D.A. Forest Service General Technical Report PNW-164.

Maser, C., Trappe, J. M. and Li, C. Y., 1984. Large woody debris and long-term forest productivity. Pp. 1–6 *in* Pacific Northwest Bioenergy Systems: Policies and Applications. Proceedings of a conference held at the Portland Marriott Hotel, May 10-11 1984. United States Department of Energy and the Pacific Northwest and Alaska Bioenergy Program.

Maser, C. and Sedell, J. R., 1994. From the Forest to the Sea: The Ecology of Wood in Streams, Rivers, Estuaries, and Oceans. St. Lucie Press, Delray Beach.

Meggs, J., 1996. Pilot study of the effects of modern logging practices on the decaying-log habitat in wet eucalypt forest in south-east Tasmania. Report to the Tasmanian RFA Environment and Heritage Technical Committee. Commonwealth of Australia and the State of Tasmania. November 1996.

Meggs, J., 1997. Logs in a state of decay. Research Note No. 2. March 1997. Forestry Tasmania, Hobart.

Meggs, J. and Taylor, R. J., 1999. Distribution and conservation status of the Mt. Mangana Stag Beetle *Lissotes latidens* (Coleoptera: Lucanidae). *Papers Proc. Roy. Soc. Tas.* **133:** 23–28.

Mesibov, R., 1986. A Guide to Tasmanian Centipedes. Published by the author, Zeehan, Tasmania.

Mesibov, R. and Ruhberg, H., 1991. Ecology and conservation of *Tasmanipatus barretti* and *T. anophthalmus*, parapatric onychophorans (Onycophora: Peripatopsidae) from north-eastern Tasmania. *Papers Proc. Roy. Soc. Tas.* **125:** 11–16.

Melville, J. and Swain, R., 1999. Home-range characteristics of an alpine lizard, *Niveoscincus microlepidotus* (Scincidae), on Mt. Wellington, southern Tasmania. *Wildl. Res.* **26:** 263–70.

Naiman, R. J. and Bilby, R. E., (eds), 1998. River Ecology and Management. Lessons from the Pacific Coastal Ecoregion. Springer-Verlag, New York.

New, T., 1995. Onychophora in invertebrate conservation: priorities, practice and prospects. *Zool. J. Linn. Soc.* **114:** 77–89.

New South Wales National Parks and Wildlife Service, 1999. Threatened Species Information. Spotted-tailed Quoll. New South Wales National Parks and Wildlife Service, Hurstville, Sydney. September 1999.

Niemelä, J., Haila, Y. and Puntitila, P., 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* **19:** 352–68.

Noel, J. M., Platt, W. J. and Moser, E. B., 1998. Structural characteristics of old- and second-growth stands of Longleaf Pine (*Pinus palustris*) in the Gulf Coastal region of the U.S.A. *Cons. Biol.* **12:** 533–48.

Noske, R. A., 1982. Comparative Behaviour and Ecology of some Australian Bark Foraging Birds. University of New England, Armidale.

O'Connell, A. M., 1997. Decomposition of slash residues in thinned regrowth eucalypt forest in Western Australia. *J. App. Ecol.* **34:** 111–22.

Økland, B., 1996. Unlogged forest: Important sites for preserving the diversity of Mycetophilids (Diptera: Sciaroidea). *Biol. Cons.* **76:** 297–310.

Ough, K. and Ross, J., 1992. Floristics, fire and clearfelling in wet forests of the Central Highlands of Victoria. Silvicultural Systems Project Technical Report No. 11. Department of Conservation and Environment, Melbourne, Australia.

Ough, K. and Murphy, A., 1996. The effect of clearfell logging on tree-ferns in Victorian wet forest. *Aust. For.* **59:** 178–88.

Owen, W. H. and Thompson, J. A., 1965. Notes on the comparative ecology of the common brushtail and mountain possums in eastern Australia. *Vict. Nat.* **82:** 216–18.

Pearce, M. H. and Malajczuk, N., 1990. Stump colonization by *Armillaria luteobubalina* and other wood decay fungi in an age series of cut stumps in Karri (*Eucalyptus diversicolor*) regrowth forests in south-western Australia. *New Phytologist* **115:** 129–38.

Peet, R. K. and Christensen, N. L., 1987. Competition and tree death. *BioScience* **37:** 586–95.

Perry, D. H., Watson, J. A. L., Bunn, S. E. and Black, R., 1985. Guide to the termites (Isoptera) from the extreme south-west of Western Australia. *J. Roy. Soc. West. Aust.* **67:** 66–78.

Pharo, E. J. and Beattie, A. J., 2002. The association between substrate variability and bryophyte and lichen diversity in eastern Australian forests. *The Bryologist* (in press).

Rab, M. A., 1992. Impacts of timber harvesting on soil disturbance and compaction with reference to residual log harvesting in East Gippsland, Victoria — a review. VSP Technical Report No. 13. Department of Conservation and Environment, Melbourne.

Rab, M. A., 1998. Rehabilitation of snig tracks and landings following logging of *Eucalyptus regnans* forests in the Victorian Central Highlands — a review. *Aust. For.* **61:** 103–13.

Rawlinson, P. A., 1975. Two new lizard species from the genus *Leilopisma* (Scincidae: Lygosominae) in south-eastern Australia and Tasmania. *Mem. Nat. Mus. Vic.* **36:** 1–16.

Read, J. and Hill, R. S., 1983. Rainforest invasion onto Tasmanian old-fields. *Aust. J. Ecol.* **8:** 149–61.

Recher, H. F., 1996. Conservation and management of eucalypt forest vertebrates. Pp. 339–88 *in* The Conservation of Wildlife Diversity in Forested Landscapes Around the Globe ed by R. M. DeGraaf and R. I. Miller. Chapman and Hall, London.

Recher, H. F., Rohan-Jones, W. and Smith, P., 1980. Effects of the Eden woodchip industry on terrestrial vertebrates with recommendations for management. *For. Comm. New South Wales, Research Note* No. 42.

Resource and Conservation Assessment Council, 2002. Terms of licence under the Threatened Species Conservation Act 1995. http:www.racac.nsw.gov.au/rfa/pdf/Eden_TSL.pdf

Rismiller, P., 1999. The Echidna: Australia's Enigma. Hugh Lauter Levin Associates Inc. Hong Kong.

Robinson, D., 1998. Lowering the goals? Habitat requirements of vertebrates and other wildlife groups in Victoria's Northern Plains and how well they match up. *In* Down to Grass Roots: Proceedings of a Conference on the Management of Grassy Ecosystems. Victorian University, St Albans, Melbourne.

Robinson, R. T., 1997. Dynamics of coarse woody debris in floodplain forests: impact of forest management and flood frequency. BSc (Hons) thesis, Charles Sturt University, Wagga.

Robertson, P., 1981. Comparative reproduction ecology of two southeastern Australian skinks. Pp. 25–37 *in* Proceedings of Melbourne Herpetological Symposium ed by C. B. Banks and A. A. Martin. Zoological Board of Victoria, Melbourne.

Rosenzweig, M. L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, United Kingdom.

Roth, L. M. and Willis, E. R., 1960. The biotic associations of cockroaches. *Smith. Misc. Coll.* **141:** 1–470.

Schodde, R. and S. C. Tiedemann (eds), 1986. Reader's Digest Complete Book of Australian Birds. Reader's Digest, Sydney.

Scott, I. A. and Rowell, D., 1991. Population biology of *Euperipatoides leuckartii* (Onychophora: Peripatopsidae). *Aust. J. Zool.* **39:** 499–588.

Seebeck, J. H., Warneke, R. M. and Baxter, B. J., 1984. Diet of the Bobuck, *Trichosurus caninus* (Ogilby) (Marsupialia: Phalangeridae) in a mountain forest in Victoria. Pp. 145–54 *in* Possums and Gliders ed by A. P. Smith and I. D. Hume. Surrey Beatty & Sons, Chipping Norton, Sydney.

Settle, G. and Croft, D. B., 1982. Maternal behaviour of *Antechinus stuartii* (Dasyuridae, Marsupialia) in captivity. Chapter 35 *in* Carnivorous Marsupials ed by M. Archer. Surrey Beatty & Sons, Chipping Norton.

Shine, R., 2001. Australian Snakes: A Natural History. Reed New Holland, Sydney.

Smith, A. P., Wellham, G. S. and Green, S. W., 1989. Seasonal foraging activity and microhabitat selection by echidnas (*Tachyglossus aculeatus*) on the New England Tablelands. *Aust. J. Ecol.* **14:** 457–66.

Smith, A. P., Moore, D. M. and Andrews, S. P., 1992. Proposed Forestry Operations in the Glen Innes Forest Management Area. Fauna Impact Statement. Supplement to the Environmental Impact Statement. Report for the Forestry Commission of New South Wales by Austeco Pty. Ltd.

Sollins, P., Cline, S. P., Verhoeven, T., Sachs, D. and Spycher, G., 1987. Patterns of log decay in old-growth Douglas-fir forests. *Can. J. For. Res.* **17:** 1585–595.

Spies, T. A., Franklin, J. F. and Thomas, T. B., 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* **69:** 1689–702.

Stamps, J. A., 1977. Social behaviour and spacing patterns in lizards. Pp. 265–334 *in* Biology of the Reptilia, Volume 7 ed by L. Gans and D. W. Tinkle. Academic Press, New York.

State Forests of NSW, 1995. Casino Management Area Environmental Impact Statement. State Forests of NSW, Sydney.

State Forests of New South Wales Northern Region, 1996. Fuel Management Plan Casino District, Northern Region State Forests of New South Wales. Murwillumbah Management Area EIS Supporting Document No. 2. Forestry Commission of New South Wales.

Statham, H. L. and Harden, R. H., 1982. Habitat utilisation of *Antechinus stuartii* (Marsupialia) at Petroi, northern New South Wales. Pp. 165–85 *in* Carnivorous Marsupials ed by M. Archer. Surrey Beatty & Sons, Chipping Norton.

Sturtevant, B. R., Bissonette, J. A., Long, J. N. and Roberts, D. W., 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. *Ecol. Appl.* **7:** 702–12.

Sverdrup-Thygeson, A., 2001. Key habitats in the Norwegian production forest: A case study. *Scandin. J. For. Res.* **16** (in press).

Svendrup-Thyseon, A. and Lindenmayer, D. B., 2002. The use of indicator species in boreal forest management. *For. Ecol. Man.* (in press).

Swan, G., 1990. A Field Guide to the Snakes and Lizards of New South Wales. Three Sisters Productions Pty Ltd, Winmallee, New South Wales.

Swift, M. J., 1977. The ecology of wood decomposition. *Science Progress* **67:** 175–99.

Tait, N. N., Stutchbury, R. J. and Briscoe, D. A., 1990. Review of the discovery and identification of Onychophora in Australia. *Proc. Linn. Soc. NSW* **112:** 153–71.

Taylor, R., 1990. Occurrence of log-dwelling invertebrates in regeneration and old-growth wet sclerophyll forest in southern Tasmania. *Papers Proc. Roy. Soc. Tas.* **119:** 7–15.

Taylor, R. J., 1991. The role of retained strips for fauna conservation in production forests in Tasmania. Pp. 265–70 *in* Conservation of Australia's Forest Fauna ed by D. Lunney. Royal Zoological Society of NSW, Sydney.

Triggs, B., 1997. Tracks, Scats and Other Traces. A Field Guide to Australian Mammals. Oxford University Press, Melbourne.

Walters, J. R., Ford, H. A. and Cooper, C. B., 1999. The ecological basis of sensitivity of brown treecreepers to habitat fragmentation: a preliminary assessment. *Biol. Cons.* **90:** 13–20.

Warneke, R. M., 1971. Field study of the Bush Rat (*Rattus fuscipes*). *Wildl. Contrib., Vic.*, No. **14:** 1–115. Fisheries and Wildlife Department, Melbourne.

Waters, J. R., McKelvey, K. S., Luoma, D. L. and Zabel, C. J., 1997. Truffle production in old-growth and mature fir stands in northeastern California. *For. Ecol. Man.* **96:** 155–66.

Watt, A., 1991. The ecology of three species of Antechinus (Marsupialia: Dasyuridae) in upland rainforests of north-east Queensland. PhD thesis, James Cook University of North Queensland, Townsville.

Watts, C. and Aslin, H. J., 1981. The Rodents of Australia. Angus and Robertson, Sydney.

Wayburn, L. A., Franklin, J. F., Gordon, J. C., Binkley, C. S., Mladenhoff, D. J. and Christensen, N. L., 2000. Forest Carbon in the United States: Opportunities and Options for Private Lands. Pacific Forest Trust, Santa Rosa, California.

Webb, G., 1985. Habitat use and activity patterns in some southeastern Australian skinks. Pp. 23–30 *in* Biology of Australasian Frogs and Reptiles ed by G. Grigg, R. Shine and H. Ehmann. Royal Zoological Society of NSW, Sydney.

Wiegel, M., 1990. Australian Reptile Park's Guide to Snakes of South-east Australia. Wiegel Photoscript, Gosford, New South Wales.

Wilkinson, D. A., Grigg, G. C. and Beard, L. A., 1998. Shelter selection and home range of echidnas, *Tachyglossus aculeatus*, in the highlands of south-east Queensland. *Wild. Res.* **25:** 219–32.

Williams, M. R. and Faunt, K., 1997. Factors affecting the abundance of hollows in logs in Jarrah forest of south-western Australia. *For. Ecol. Man.* **95:** 153–60.

Wilson, S. K. and Knowles, D. G., 1988. Australia's Reptiles. A Photographic Reference to the Terrestrial Reptiles of Australia. Collins Publishers, Sydney.

York, A., 1996. Long-term effects of repeated prescribed burning on forest invertebrates: Management implications for the conservation of biodiversity. Pp. 181-259 *in* Australia's Biodiversity — Responses to Fire. Plants, Birds and Invertebrates ed by A. M. Gill, J. C. Woinarski and A. York. Environment Australia Biodiversity Technical Paper **1:** 1-266.

Williams, J. E. and Gill, A. M., 1995. The impact of fire regimes on native forests in eastern New South Wales. *Environmental Heritage Monograph Series* No. 2. New South Wales National Parks and Wildlife Service, Sydney.

Woldendorp, J., 2000. Estimating carbon in mature eucalypt forests. BSc (Hons) thesis, Department of Geography, The Australian National University, Canberra.

Yoneda, T., 1986. Decomposition of wood litter in a forest. *Jap. J. Ecol.* **36:** 117–29.

Young, A. M., 1986. Common Australian Fungi. New South Wales University Press, Kensington.