Bell-miner-associated dieback: an ecological perspective

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Summary

An interpretation of dieback within eucalypt forests might take account of (i) the consequences of the rapid evolutionary expansion of the eucalypt progenitor associated with continental drift; (ii) the nature of species patterns and pattern–environment relationships within the forests; (iii) the significance of stand structures and ecosystem processes in maintaining stable eucalypt forests; (iv) the destabilisation of forests and ecosystem processes associated with recurrent fires in the post-settlement period and the logging of the forests; and (v) specific site factors which may predispose disturbed ecosystems to decline, insect predation and dieback.

Keywords: dieback; fire ecology; biological activity in soil; ecological disturbance; bell miners; psyllids; *Eucalyptus*; Australia

Introduction

Factors contributing to bell-miner-associated dieback (BMAD) are largely unresolved (Wardell-Johnson *et al*. 2005, this issue). However, we may provisionally accept that dieback is related to complex interactions between forest disturbance, changes in stand structure, absence of regular burning, development of a dense understorey, increase in foliar nutrients, infestation of tree crowns by a sap-sucking psyllid, and the aggressive colonisation of the forest by the bell miner (Jurskis 2005; Stone 2005; Turner 2005; Wardell-Johnson *et al*. 2005; and all this issue).

Why is this happening? This paper argues that BMAD is one of a series of eucalypt dieback events which have occurred in all Australian states, and that some form of stress or imbalance between forest community and site is a common thread running through them. The paper attempts to address the basic questions: why are eucalypts subject to environmental stress, and under what circumstances may this be expressed? In so doing it takes account of the evolutionary origins of the eucalypts, species patterns and ecosystem processes, and the effects of post-settlement perturbations on them. Bell-miner-associated dieback is discussed in these terms.

Dieback in eucalypt forests

Species patterns and their environmental relationships

An interpretation of dieback might start with an appreciation of the evolutionary pressures which created the eucalypt and ensured its dominance of all but the driest parts of an entire continent. The progenitors of the eucalypt had an outstanding evolutionary capacity to keep pace with the dramatic environmental changes associated with continental drift, notably the break-up of the rainforest cover, declining soil fertility and a drying climate. As a result, present-day forests can be interpreted in terms of a progressive and sensitive replacement of eucalypt subgenera and species along environmental gradients, including those in soil fertility, soil physical properties and water status (Florence 1996, Ch. 2). Consistent and environmentally sensitive community patterns suggest that, for any one site, ecosystem stability may have depended on maintaining a balance between the availability of site resources and the demand on those resources, and on the maintenance of natural ecosystem processes. Hence, in examining eucalypt dieback it is appropriate to start by considering the disturbances to community patterns and ecosystem processes associated with European settlement.

Effects of post-settlement fires and logging

Effects on stand structure and demand for site resources

At European settlement, widely spaced, large-boled trees generally dominated eucalypt forests. Nevertheless, many forests were uneven-aged, i.e. regrowth developed from time to time within gaps created by the senescence or death of individual trees or small patches of trees. Relatively light Aboriginal-type burning and lightning fires contributed to the maintenance of an open and sometimes grassy forest floor through much of the forest.

Following settlement, the bush was regularly burned to protect the pioneering properties and to provide rough grazing for stock. Sometimes these fires became conflagrations of great intensity. Moreover, much of the forest has been logged and, from the early 1900s, attempts were made to impose complete protection regimes. These events generated a more complex structure, including a greater component of even-aged regrowth, a more persistent shrubby understorey and high fuel loads.

Rapidly developing even-aged regrowth will make a much greater demand on site resources than uneven-aged old-growth forest, particularly around the peak growth phase (Florence 1996, Ch.13). This occurs as early as 6–10 y in some fast-growing species, and from 15–35 y in many other species. Where the regrowth stand is heavily stocked and site resources are limited, possible consequences can be reduced stand vigour, weak expression of dominance, and stand stagnation. The forest may be particularly sensitive to stress where there has been an increase in the frequency of a more site-demanding species.

Effect of fire and logging on ecosystem processes

A fully stocked eucalypt forest influences soil biological processes through the incorporation into the soil organic matter of large quantities of 'woody' litter (leaves, twigs, bark and capsules) with a high C:N ratio and low nutrient status. While there will be an increase in soil organic matter and soil nutrients during the rapid growth phase, the amount of available carbon energy may eventually be insufficient to drive healthy microbial processes. As a result, the rate of nutrient mineralisation will decline and a plant-antagonistic microflora may develop (Florence 1996, Ch. 3). These processes, along with a high rate of water use and occasional low-intensity fire, helped maintain the forest in an open, stable condition.

In nature, an occasional fire of greater intensity would re-stimulate soil microbial processes, generate a flush of available nutrients and, through soil-stored seed, re-establish a shrubby understorey, including soil ameliorating species such as the wattles. Similarly, in silvicultural practice, intense fire is used to create a seedbed for eucalypt regeneration by stimulating soil biological processes in long-undisturbed or lightly-burned forest.

The greater frequency of severe wildfires and logging following European settlement affected not only stand structures but also the ecosystem processes helping to maintain open, stable communities. Nutrient and other soil biological processes were no longer regulated to the same extent. The level of available soil nutrients increased, a vigorous and more persistent shrub understorey developed, and the conditions under which low-intensity fire could readily and widely burn through the forest no longer applied.

An interpretation of some dieback events in eucalypt forests

Against this background, a tentative interpretation of a number of eucalypt dieback events is presented:

- *heavy cutting and burning of the old-growth and essentially uneven-aged messmate stringybark/peppermint forests in the goldfields region of central Victoria.* In this case the resulting even-aged regrowth forest (possibly with a greater component of the more site-demanding messmate stringybark) may have been subject to environmental stress from around 15–30 y of age; i.e. the high demand phase and the stand age at which dieback is first observed (Edgar *et al.* 1976). Messmate stringybark may be susceptible to *Armillaria* where it is in a physiologically weakened condition.
- *southern regrowth dieback in Tasmania.* This dieback was mainly associated with highly stocked regrowth (largely messmate stringybark), again commencing around the time of peak demand on site resources. Dieback developed either following clearfelling, slash burning and seeding, or following severe wildfire alone (Podger *et al.* 1980). Dieback may have been associated with insufficient water and *available* nutrients to maintain the vitality of the heavily stocked forest, particularly during the droughts which predated the onset of dieback in the 1960s. Tree decline might also have been accentuated by the accumulation of heavy litter loads, protection from periodic light burning, and increasingly unfavourable soil microflora.
- *incidence of bullseye borer in karri.* This is not a conventional dieback event, but the principle remains the same. Stem borer infestation of 25–30-y-old karri regrowth (from clearfelling, slash burning and seeding) is greater on poorer than on high-quality sites, and drier sites (formerly with mixtures of karri, marri and jarrah) are more prone to borer attack (Farr *et al.* 2000). This again might be attributed to enhanced environmental stress associated with changes in stand structure and the frequency of component species (notably a greater component of even-aged karri), excess demand on limited site resources around the peak demand phase, high litter loads and inadequate burning.
- *dieback in the jarrah forest.* Jarrah dieback is attributed to the pathogen *Phytophthora cinnamomi.* A related hypothesis (Davison 1997) suggests dieback might be attributed in the first instance to reduced soil aeration or waterlogging. This could be associated with an increase in the frequency of severe fires, weakening of the canopy trees, the harvesting of forests, reduced canopy transpiration and resultant changes in the soil water profile. It is under these circumstances that jarrah might be increasingly susceptible to *P. cinnamomi.*
- *high-altitude eucalypt dieback in Tasmania.* Decline of alpine ash has been attributed to the cessation of regular Aboriginal burning and the development of a temperate rainforest understorey. This understorey appears to create soil conditions which are antagonistic to alpine ash, generating premature tree decline and death (Ellis *et al.* 1980). Ellis and Pennington (1992) have shown that alpine ash seedlings raised in a glasshouse are increasingly inhibited when grown on soils taken from a number of successional stages towards temperate rainforest, that is, in this case, the development of a mesic understorey could have a direct and negative effect on the health of alpine ash.
- *dieback of woodland trees (rural or New England dieback).* Several factors contribute to dieback of woodland trees, principal among them being higher levels of nutrients in soils (particularly where associated with pasture improvement), high foliar nitrogen contents, insect outbreaks, rapid leaf turnover, drought and, associated with partial woodland clearing, reduced populations of insectivorous birds. This emphasises the sensitivity of eucalypts to changes in soil fertility and the soil microflora.

This summary suggests that eucalypts can be sensitive to a wide range of factors following stand disturbance. These include: (i) various site conditions predisposing eucalypts to environmental stress, (ii) excessive demand on site resources associated with changes in stand structure, (iii) an increase in the frequency of more-site-demanding species, (iv) changes in the soil microflora and increased rates of nutrient mineralisation, (v) a more persistent shrub understorey, (vi) greater soil wetness and reduced soil aeration, and (vii) the activity of pathogenic or antagonistic soil organisms.

It is against this background that we can address BMAD.

An interpretation of bell-miner-associated dieback in the eucalypt–rainforest interface

Much of the BMAD occurs within moist (wet sclerophyll) eucalypt forest — though it has been extending into more open forest as a mesic (rainforest element) understorey develops. The principles underpinning species patterns and ecosystem processes within the eucalypt–rainforest interface are similar to those relating to the eucalypt sclerophyll forest generally. Nevertheless it is worth emphasising a number of key points with particular relevance to the interface zone.

Species pattern–environment relationships

There are consistent community–environment patterns within the interface — despite the role fire undoubtedly has played in maintaining mixed eucalypt–rainforest communities. For example, blackbutt (subgenus *Monocalyptus*) is one the first species to be excluded along the soil fertility gradient, despite its well-known responsiveness to fire. Blackbutt may be less competitive on soils of higher fertility (Florence 1996, Ch. 5), or it may be increasingly sensitive to soils with high nutrient levels and a complex microbial environment. *Symphyomyrtus* species (including grey ironbark, grey gum, spotted gum, flooded gum and Sydney blue gum) extend further along the soil fertility gradient. Many of these species in turn drop out, leaving tallowwood and the non-eucalypt (but Myrtaceous) brush box as the main emergents from near fully-developed rainforest. As in the eucalypt sclerophyll forest, there may be circumstances where it is ecologically inappropriate to radically alter the natural species patterns and species frequencies.

Role of ecosystem processes in maintaining eucalypt sclerophyll–rainforest boundaries

Conventional wisdom holds that lightning fires and regular burning by Aboriginals created more clearly defined forest boundaries than are apparent today, and maintained a more open forest floor. An alternative view is that the sharper boundaries were related *primarily* to the effect a complete eucalypt canopy has on soil conditions, i.e. a high rate of water use, the incorporation into soil of a large amount of high C:N ratio litter, and the negative influence this can have on the soil microflora, nutrient mineralisation and other soil biological processes. In the absence of major perturbations, this eucalypt–soil interaction, together with periodic low-intensity fire, may have limited the development of a rainforest understorey and helped maintain relatively open, stable interface communities.

Impacts of post-settlement disturbance

Greater frequency of more intense fire, and then logging, following settlement would have weakened the site control exerted by the old-growth eucalypt canopy and destabilised natural processes. It is likely there would have been a substantial increase in the rate of soil nutrient mineralisation and a greater uptake of nutrients by residual and regrowth eucalypts. The increase in soil nutrients would help generate colonisation by a rainforest element (mesic) understorey, and this, in turn, would help sustain more rapid nutrient turnover. There would be in this way a more or less permanent increase in available soil nutrients. Other consequences of settlement have often included a highly disturbed overwood canopy (patchy tree regeneration and a reduced tree stocking), and a change in the relative frequency of component species.

Cumulatively, these changes represent a substantial departure from the regulated environment of the pre-settlement forest. These are changes which can enhance the habitat for bell miners and conditions for psyllid infestation through disturbed canopies, limited eucalypt regeneration, dense shrub understorey, and vigorous tree foliage with high nutrient levels (Stone 2005, this issue).

Discussion

Wardell-Johnson *et al.* (2005, this issue) explore many factors contributing to BMAD, and almost invariably point to serious deficiencies in the information base, inadequate research, or inadequate quantification or testing of hypotheses. To better understand the dieback phenomenon, this paper has presented an hypothesis based on an appreciation of the evolutionary origins of the eucalypts, patterns and processes within eucalypt forests, and the impact of sustained disturbance on them.

Taking a broad perspective, BMAD may reflect problems created by the overlap of vegetational systems with contrasting evolutionary origins and environmental adaptations. Notably, the rainforests occupy the most fertile of the east coast soils, and for the eucalypts, rapid evolutionary development was in the direction of less fertile and drier soils.

There is undoubtedly a continuing ‘struggle’ for site occupancy by the two systems with the continuing dominance of eucalypts dependent both on periodic fire and on the extent to which they can regulate soil biological processes and nutrient mineralisation within the overlap zone. Where destabilised by post-settlement fire and logging, changes in ecosystem processes may have exposed the limits of the eucalypts’ capacity to cope with soils with consistently high levels of available nutrients. Perhaps this is related to the way eucalypts growing on infertile soils take up nutrients opportunistically when available (e.g. following fire), and store them within the foliage, phloem and mobile sapwood pool (Florence 1996, Ch. 2).

Several interpretations of BMAD are consistent with these concepts. Jurskis and Turner (2002) and Jurskis (2005, this issue) argue that post-European land management, notably the failure to regard fire as an integral component of the eucalypt ecosystem, is altering the environment so that soils supporting natural tree communities have become unnaturally moist and fertile, and dense mesic shrub layers have developed. This has affected the soil microbial environment and root dynamics of eucalypts, and impaired their health. The concepts are also consistent with the role of increased nitrogen mineralisation and high foliar nutrient levels in BMAD (Turner and Lambert 2005, this issue). The study by Stone (2005, this issue) shows that eucalypt stands susceptible to bell miner colonisation often occur on relatively fertile soils which support a dense shrubby understorey.

We do not know whether the development of a dense understorey will, in itself, create the conditions for psyllid infestation. There is much healthy eucalypt forest with a dense mesic understorey, sometimes contiguous with dieback forest. In this case, the critical questions to be resolved are these: is all disturbed interface (wet sclerophyll) forest vulnerable to psyllid infestation and dieback, or will dieback occur only where a number of specific and as yet unresolved environmental factors are involved? If the latter, it will be a key research challenge to identify these factors. Some preliminary ideas follow.

Stone (1996) suggests primary predisposing stresses might include significant climatic perturbations, site quality (or tree species growing off-site), the inherent susceptibility of some tree species and age structures, and stand disturbance (including logging and fire history). 'Tree species growing off-site' might be extended to include those situations where there has been an increase in the frequency of faster-growing species capable of accumulating high levels of foliar nutrients and supporting high insect loads (e.g. Sydney blue gum). Wardell-Johnson and Lynch (2005, this issue) describe a situation where widespread and severe dieback is associated with a heavy-textured sandstone-derived soil overlain by a veneer of basalt-derived soil. A nutritionally enriched heavy-textured soil might be a predisposing factor in this case.

We should also consider the extent to which attributes of root systems may predispose a stand to decline and dieback. Some species within the interface zone are essentially adapted to drier environments or shallower or poorly structured soils (including grey ironbark, grey gum, white mahogany and spotted gum). The root configuration of these species may place greater emphasis on more deeply penetrating roots than on finer, near-surface roots, as in spotted gum (Neave and Florence 1994). Where the forest ecosystem is destabilised and a mesic understorey develops, root efficiency might be impaired, particularly on shallower, heavy-textured or poorly structured soils. This may limit the tree's capacity to respond to changes in nutrient availability, and/or accelerated wetting-drying phases.

Under certain soil conditions the tree could be susceptible to *Phytophthora* and other disease organisms. *Phytophthora* has been isolated from psyllid-affected stands of Sydney blue gum (Stone *et al.* 1995), though this organism is also widely distributed in healthy coastal forest in NSW.

These concepts create a preliminary framework in which we might establish continuing research directions and begin to formulate rehabilitation operations. There are substantial areas of highly disturbed (inadequately stocked) interface (wet sclerophyll) forest along the east coast of Australia (Florence 2005), much of which may be vulnerable to BMAD. If we are to truly embrace environmental conservation, state-wide research and rehabilitation programs are both essential and urgent.

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