Bell-miner-associated dieback at the tree crown scale: a multi-trophic process

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Summary

This paper examines some of the factors and processes which interact within eucalypt stands affected by bell-miner-associated dieback. A key symptom of this form of dieback is sustained foliar damage from herbivorous insects, in particular psyllids. Repeated cycles of defoliation/refoliation result in branch death and crown contraction. Weakened trees become more susceptible to secondary stressors such as wood borers, soil fungal pathogens and abnormal levels of soil moisture. Psyllid outbreaks can occur through a reduction in the efficacy of their natural enemy complex, and the provision of sufficient favourable foliage to sustain high insect populations. The young foliage preferred for feeding and oviposition by most eucalypt insect herbivores can occur when soil moisture and nutrients and canopy irradiation are non-limiting. Bell miner colonies require high insect densities in their food source and they reinforce this situation through their feeding behaviour and territorial defence. The study suggests the effect of bell miners on the populations of herbivorous insects, and hence the amount of insect-damaged foliage, is density dependent. Bell miners also require dense understorey, about 2–5 m high, for nesting sites, and the presence of surface water. Any management practice that reduces bell miner density will in turn reduce the density of insect herbivores and hence foliar damage in the eucalypt tree crowns. Then, if the trees have not become too debilitated, crown recovery is likely to occur.

Keywords: forest management; dieback; herbivores; bell miner; *Manorina melanophrys*; psyllids; *Eucalyptus*; Australia

Introduction

Bell-miner-associated dieback (BMAD) refers to the form of canopy decline observed in eucalypt crowns occupied by feeding bell miners (*Manorina melanophrys*).

Bell miners are insectivorous birds typically living in large colonies of up to 200 birds and at relatively high densities (Bower 1998; Clarke and Schedvin 1999; J. Shields and E. Kemmerrer, Forests NSW, unpublished data). Bell miners display aggressive interspecific behaviour (Poiani *et al.* 1990; Clarke and Fitz-Gerald 1994). Sites with bell miners often have a greater density of birds than similar sites lacking bell miners, but they have a lower diversity of bird species (Bower 1998; Clarke and Schedvin 1999).

This paper discusses factors and processes associated with BMAD operating at the tree crown/stand scale. Factors that become important at the landscape scale, such as forest fragmentation and forest management practices, are discussed in other papers in this issue of *Australian Forestry*.

Site factors

As part of the Bell-miner Associated Dieback Strategy (NSW National Parks and Wildlife Service 2004) a multi-agency research project was initiated in a 30 000 ha study area containing BMAD-affected forests in the Richmond Range, northern NSW. Twenty-four field plots, with a 20 m radius, exhibiting a range in floristic composition, stand structure and canopy condition were established. Detailed plot data on the floristic composition, per cent crown cover of both the overstorey and understorey, tree crown structure and condition, bell miner density, soil chemistry and soil profile descriptions were collected in August 2004.

Five soil samples taken at a depth of 15 cm from each plot centre and cardinal points were bulked and mixed before being sub-sampled to 500 g and placed into a refrigerated Esky. Within three hours the soil samples were delivered to the Diagnostic and Analytical Services Environmental Laboratory at Wollongbar, NSW. The samples were placed immediately into a dehydrater before being analysed by standard analytical methods (Rayment and Higginson 1992; Clescerl *et al*. 1998) to determine soil pH, total organic carbon (%), exchangeable cations (Al, Ca, K, Mg, Na), available phosphorus (Bray), mineral nitrogen, ammonium nitrogen and nitrate nitrogen.

Multidimensional scaling ordination (Belbin 1995) of the floristics data revealed that neither mean tree crown condition nor bell miner density were closely related to the floristic species composition of the plots (D. Binns, Forests NSW and G. Wardell-Johnson, University of Queensland, unpublished data). The major ordination pattern broadly separates plots into those containing moist/mesic overstorey and understorey species, and those tending to have drier sclerophyll species, often with a grassy understorey. Poorer tree crown condition and higher bell miner density tended to be associated with the mesic plots. This lack of close association with floristic composition may contribute to the distribution of bell miners from southern Victoria to south-eastern Queensland (Pizzey 1989). The relative susceptibility of forest types in terms of the rate of tree decline has not been investigated; possibly, certain types may decline more rapidly than others (e.g. Stone *et al.* 1995). Therefore, successful bell miner colonies can occur in a range of eucalypt forest types but typically in mesic eucalypt forests supporting a dense shrubby understorey suitable for nesting (e.g. McCulloch and Noelker 1974; Smith and Robertson 1978; Higgins *et al*. 2001). The significance of forest structure influencing bell miner populations is not unique. In a survey of birds across a range of woodland plots, Gilmore (1987) concluded that the composition of insectivorous bird communities was largely determined by the structure of stand vegetation.

Irrespective of the floristic species, composition and stand structure, the literature also indicates that affected eucalypt stands tend to be located mainly in foothills, valleys and gullies, and on riverbanks or floodplains (e.g. McCulloch and Noelker 1974; Loyn 1987; Clarke and Fitz-Gerald 1994). A significant linear relationship between soil ammonium content (NH_4-N) and mean tree crown condition has been demonstrated using data from the same 24 Richmond Range plots ($r_p = -0.64$, $P > 0.001$, $n = 24$). The apparent association between high site fertility (i.e. relatively high soil ammonium content and a low soil carbon:nitrogen ratio), unhealthy eucalypt crown condition and high bell miner density is illustrated in Figure 1. Based on the data from these plots, it appears that eucalypt stands susceptible to bell miner colonisation often occur on relatively fertile sites and support a dense shrubby understorey (Fig. 1). From soil profile descriptions undertaken at each plot, including a categorical assessment of soil permeability

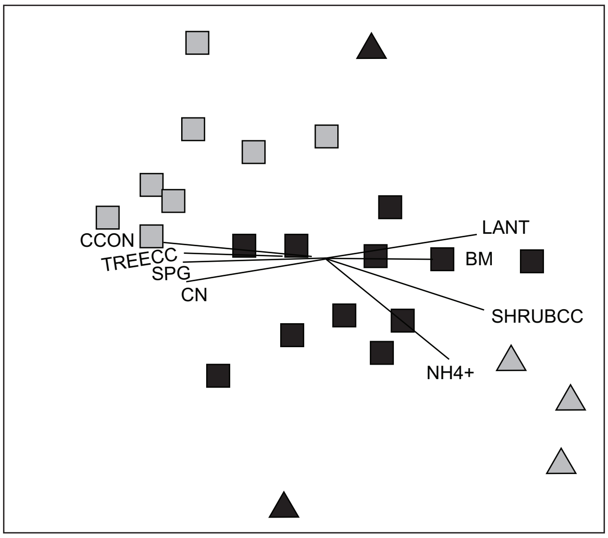

Figure 1. Two-dimensional Multidimensional Scaling Ordination (SSH MDS, Stress 0.14, cutoff 0.9) based on six stand and tree structural attributes, collected from 24 20-m-radius plots located in the Richmond Range, northern NSW. Four plot groups are shown by different symbols. Only the two smallest site groups are not significantly different (ANOSIM, $P < 0.05$) from one another (Bray–Curtis metric, UPGMA, $b = -0.1$). Biplots (PCC, MCAO) of all intrinsic variables are significantly correlated ($P < 0.05$) with ordination axes. Three of the structural attributes: eucalypt crown condition (CCON, high values = healthy crowns), tree crown cover (TREECC), shrub cover (SHRUBCC) are shown. Five extrinsic variables significantly correlated with ordination axes are also shown (Bell miner density = BM, abundance of *Lantana camara* = LANT, abundance of *Corymbia variegata* = SPG, soil ammonium content = NH_4^+, soil carbon/nitrogen ratio = CN).

and soil drainage (D. Moran, landscape soil surveyor, Department of Infrastructure, Planning and Natural Resources, Alstonville), there was no significant association between mean crown condition and soil permeability at these sites ($r_s = 0.07$, $P = 0.7$, $n = 24$), nor between crown condition and soil drainage ($r_s = -0.03$, $P = 0.87$, $n = 24$).

'Top-down' factors

A diverse range of insects live on foliage in crowns colonised by bell miners, but herbivorous insects, especially sap-sucking psyllids, are usually the most abundant (Stone 1996). All environmental systems possess food webs that operate at two or more trophic levels (Price *et al*. 1980). Organisms within a trophic level, such as herbivorous insects, are influenced by intra- and inter-specific competition and by 'top-down' and 'bottom-up' effects. For example, natural enemies regulate insect herbivores through top-down effects while the quantity and quality of foliage are bottom-up effects (e.g. Clark 1964; Price *et al.* 1980; Gratton and Denno 2003). I argue that there are two ways bell miners significantly influence the top-down processes which regulate the population dynamics of herbivorous insects in eucalypt trees: i.e. through their territoriality and their feeding behaviour.

Territoriality of bell miners

Bell miners are extremely efficient at excluding other bird species from their communally defended territory, including other insectivorous birds (e.g. Clarke and Schedvin 1999). Removal of bell miners from a stand of *Eucalyptus radiata* near Healesville, Victoria, resulted in an immediate influx of other bird species, although the numbers decreased after a few weeks as the psyllid population was reduced (Clarke and Schedvin 1999). Through long-term monitoring of their study sites, Clarke and Schedvin also found bell miners were capable of establishing a small colony before psyllid numbers reached high damaging levels, and that after bell miners had gained control of the site psyllid numbers rose substantially.

Invertebrate predators and parasitoids of psyllids

Although psyllids and their carbohydrate lerps dominate the diet of bell miners, the miners also consume other invertebrates present on the foliage, including spiders, parasitic wasps and predatory insects (Campbell and Moore 1957; Poiani 1993b). Stone (1996) proposed that bell miners not only interfere with the efficacy of other insectivorous birds through aggressive interspecific territoriality, but also through their consumption of the invertebrate predators and parasitoids. Other bird species that are also generalised insect feeders (e.g. species of pardalote) do not normally occur at the densities observed for established bell miner colonies (Bower 1998; Clarke and Schedvin 1999). Therefore, reduction in invertebrate natural enemies of psyllids may be a numerical response to high bell miner populations. The release of herbivorous insects from the regulatory control of natural enemies enables their populations to increase, in particular those insect species that have several generations per year. Species of *Glycaspis* can have up to six or seven generations per year (Moore 1961). This helps explain observations by Ewen *et al.* (2003), while monitoring bell miner colonies in the same *E. radiata* forest as Clarke and Schedvin (1999), that for newly founded colonies, the increase in relative lerp density was not immediate but was significant within one year.

In addition to this temporal effect, a single bird census undertaken in the 24-plot Richmond Range study site revealed a negative linear correlation between the plot means of eucalypt crown condition and bell miner density ($r = -0.75$, $P > 0.001$, $n = 24$; D. Charley, Department of Environment and Conservation, August 2004, unpublished data). This suggests that the effect of the bell miners on the herbivorous insect populations, and hence the amount of insect-damaged foliage, is density dependent. Therefore, sites that have the potential to support high densities of bell miners are at risk of significant crown damage from insectivorous insects, while tree crowns with the potential to support lower bell miner densities are at less risk from this form of damage.

Clark and Dallwitz (1975) studied several psyllid species on *E. blakelyi* and concluded that psyllid populations were regulated at low densities by predation and at high densities by the deterioration of available preferred foliage. Local climate and environmental resources have an over-arching influence on factors operating on all the trophic levels. Therefore, changes to either local climatic conditions or the abundance of environmental resources (e.g. light intensity, soil moisture or soil nutrition) can alter the complex balance of interactions between the trophic levels and provide the potential for some herbivorous insect species to escape from low abundance ('top-down') regulation and shift into a higher abundance, but less stable, phase.

'Bottom-up' factors

Bottom-up factors are largely attributes of tree crowns, tree foliage and the nutrient status of foliage.

Leaf production and foliar nutrition

Most eucalypts have seasonal patterns of new leaf production but many are also opportunistic, responding quickly to pulses of resources such as nutrients, rainfall and light (Landsberg and Cork 1997). The majority of invertebrates and vertebrates feeding on eucalypt foliage prefer young foliage (Landsberg and Cork 1997). Both young expanding eucalypt foliage and juvenile epicormic (replacement) foliage are softer (e.g. lower lignin content) and contain higher levels of soluble nitrogen than mature foliage (e.g. Journet and Cochrane 1978; Kavanagh and Lambert 1990; Marsh and Adams 1995). *Glycaspis* psyllids, commonly abundant on foliage in crowns colonised by bell miners, lay their eggs on flush foliage. White (1969) postulated that psyllid populations are very sensitive to increases in available foliar nitrogen while other authors suggest the success of young instar herbivorous insects is directly influenced by leaf toughness (e.g. Howlett *et al.* 2001). Both these foliar attributes are favourably presented in young foliage.

In addition to the influence of leaf age, foliar nutrition has also been found to be positively correlated with higher site quality (Specht and Rundel 1990; Recher *et al.* 1996; Wright *et al.* 2001). Therefore, it is proposed that fast-growing eucalypts on high-quality sites have the capacity to carry large populations of herbivorous insects (Recher *et al.* 1996), especially if competition for resources by the host plants is reduced (e.g. Coley *et al.* 1985).

Abundance of foliage

The quantity of favourable foliage in a crown or stand of trees is an important determinant of insect abundance (Clark 1964; Ohmart *et al.* 1987). Environmental stress, such as drought, can cause an increase in the mobilisation of soluble nutrients including free amino acids such as proline, and improve the nutritional quality of foliage (Miles *et al.* 1982; Brodbeck and Strong 1987). Many eucalypts also respond to environmental stress by reducing transpiration and photosynthesis (e.g. Whitehead and Beadle 2004). In this case new foliage production is minimal or absent, limiting the quantity of preferred foliage (Clark and Dallwitz 1974; Pook 1985; Honeysett *et al*. 1992). Alternatively, any increase in crown volume, supporting a high proportion of preferred foliage, provides larger feeding surfaces for both herbivorous insects and insectivorous birds (Pearce *et al.* 1995). In a closed canopy, crown leaf production can be induced by increased canopy penetration of solar radiation (Sands 1996; Pinkard *et al*. 1998; Medhurst and Beadle 2000). This can occur through windthrow, reduced tree density, and edge effects from roads or rural/urban clearings. Many studies have reported a positive response by sap-sucking insects to 'sunnier' sections of tree crowns (e.g. White 1970; Majer *et al*. 1992). An open canopy has a higher proportion of sunlit crowns than a closed canopy. The enhanced foliar production and photosynthesis in the mid and lower sections of *E. nitens* crowns following thinning disappeared after canopy closure (Medhurst 2000).

Sustained foliar grazing

Initially, tree crowns colonised by bell miners may be vigorous where they have a high proportion of young foliage capable of supporting high insect densities. However, continued exposure to the bell miners results in persistent foliar damage from the herbivorous insects. The continued initiation and growth of replacement foliage depletes the tree's carbohydrate reserves (Bamber and Humphreys 1965) resulting in branch death and crown contraction. As epicormic replacement foliage is also of high quality as a food source for herbivorous insects (e.g. Landsberg 1990), elevated insect populations can be maintained for several seasons. Affected trees become weakened and more susceptible to secondary stressors such as wood borers and fungal decay (Moore 1962; Old *et al.* 1990). High densities of herbivorous insects, such as psyllids, are finally forced into decline through the reduction of suitable foliage (Clark and Dallwitz 1975). This culminates in the bell miners abandoning the declining tree crowns (Ewen *et al.* 2003).

Conclusion

Favourable bottom-up factors (host plant resources) do not always result in high insect abundances if other regulatory processes are in equilibrium (Price *et al.* 1980). This is evident in vigorously growing regrowth stands on moist, high-quality sites not colonised by bell miners. If bell miners are responsible for a breakdown in the top-down processes maintaining the insect herbivore populations at non-damaging levels, then management options could concentrate on reducing or removing at least one of the habitat factors favoured by bell miners. For successful colonisation, bell miners require a relatively open overstorey canopy on a site where soil moisture, soil nutrition and light penetrating the canopy are non-limiting. Under these circumstances tree crowns are likely to be vigorously growing and have the intrinsic potential to support high insect numbers. They also require a dense understorey providing suitable nesting sites and the presence of surface water (e.g. McCulloch and Noelker 1974; Pizzey 1989). An optimal height of the understorey for nesting is about 2–5 m (e.g. Smith and Robertson 1978; Clarke 1988; Poiani 1993a).

It is concluded that BMAD is an outcome derived from the presentation of a set of multi-trophic circumstances operating at the stand scale which the colonising bell miners are able to exploit. Broader landscape processes also influence the extent and severity of BMAD and these must be considered when developing management strategies. This infers a range of solutions will eventually be applied to the management of bell-miner-associated dieback.

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