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Hollow futures? Tree decline, lag effects and hollow-dependent species

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Abstract

Tree hollows are a critical breeding resource for many organisms globally. Where hollow-bearing trees are in decline, population limitation can be a serious conservation issue. A particular problem in addressing hollow limitation is the long time that hollows take to form. This means there can be a significant lag time between detecting a species' population decline and arresting the lack of hollows through reducing tree mortality and increasing regeneration. Once underway, declines of hollow-dependent species therefore can be difficult to halt. It is imperative that we identify and anticipate such future problems before they occur, and implement conservation action in advance. In this study, we use a novel application of an established modelling method to explore this issue and illustrate an 'early warning' approach, focusing on a case study of the vulnerable superb parrot *Polytelis swainsonii* from south-eastern Australia. The species is dependent on hollow-bearing trees for nesting that have a very long generation time (> 120 years). Potential nest trees for the superb parrot are on a trajectory of decline. We modelled the future hollow resource for this species under different management scenarios including: (a) business-as-usual – that is, no further specific conservation action; (b) and (c) waiting until considerable further reductions (90 and 70%) in hollows before implementing conservation actions to redress loss of hollows; and (d) implementing enhanced conservation actions now to redress loss of hollows. We found that all scenarios except (d), 'conservation action now', resulted in substantial declines in potential nest trees, and came at significant opportunity cost in terms of reducing tree mortality and increasing tree regeneration. Delaying conservation action will greatly increase the long-term risk of extinction of hollow-dependent species such as the superb parrot. Predicting and slowing the decline in available hollows by early intervention and restoration management is critical, even where hollow-dependent species populations may appear to be secure in the short-term.

Introduction

Tree hollows provide a critical breeding resource for many organisms globally. For example, across Europe, North America, Southern Africa and Australia, 18% of bird species use hollows for nesting, and 11% are obligate users (Newton, 1994). In situations where tree populations are in decline, the associated reduction in hollow availability has been associated with a decline in hollow-using species (Newton, 1994; Gibbons & Lindenmayer, 2002; Marsden & Pilgrim, 2003; Aitken & Martin, 2008; Heinsohn *et al.*, 2009).

Reversing decline in population of hollow-bearing trees is complicated by 'lag effects'. These describe the delay between initiation of actions to halt and reverse tree decline, and the time needed for trees to be old and large enough to produce suitable hollows (> 120 years) (Manning, Lindenmayer & Barry, 2004; Gibbons *et al.*, 2008). Lag effects have serious implications for threatened, hollow-dependent species (Saunders *et al.*, 2003; Maron, 2005), potentially resulting in an 'extinction debt' (Tilman *et al.*, 1994), that is, future extinction is inevitable without action now. Delay in beginning tree protection and restoration risks producing increasingly long, hollow-limited population bottlenecks in

the future, because of the long time it takes for hollows to form (Manning *et al*., 2004; Gibbons *et al*., 2008). This has direct, long-term implications for populations of hollow-dependent species.

Here, we explore the role of lag effects on the availability of potential nest trees of an obligate hollow-using species, namely the vulnerable superb parrot *Polytelis swainsonii*, in south-eastern Australia. A key challenge in planning conservation action for hollow-dependent taxa is to predict which species will be at risk from future hollow scarcity. Population estimates and simple extrapolation of trends based on passive monitoring can sometimes have limited predictive power (Lindenmayer & Likens, 2010). To predict long-term conservation risk, some understanding of ecological processes affecting critical resources that limit populations of a given species is essential. We examined a key ecological process by modelling recruitment and mortality of populations of potential nest trees for the superb parrot. Our aim was to explore the possible risks of delaying conservation actions to protect and restore hollow-bearing trees. We used an established method for modelling scattered tree populations (Gibbons *et al*., 2008; Fischer *et al*., 2010; Gibbons, McElhinny & Lindenmayer, 2010) to simulate and predict future hollow scarcity under different conservation scenarios. Our key questions were:

(1) What is the effect of current management practices on potential nest trees if these practices continue into the future?

(2) What is the effect of delaying tree conservation and restoration actions until potential nest tree populations drop substantially (by 70–90% of current levels)?

(3) What is the effect of immediately acting to reduce potential nest tree mortality and increase recruitment?

Our analysis provides an 'early warning' approach that can be adapted to other obligate hollow-nesting species.

Materials and methods

Study species

The superb parrot (weight 130–160 g, wingspan 53–57 cm, length *c*. 40 cm) occurs in a restricted range in south-eastern Australia (Webster, 1988; Webster & Ahern, 1992; Higgins, 1999). It nests in hollows in branches and tree trunks, and breeds between September and December (Webster, 1988; Webster & Ahern, 1992; Manning *et al*., 2004).

Across a significant part of its range, the superb parrot breeds in agricultural landscapes with scattered hollow-bearing trees (Manning *et al*., 2004). These trees are remnants from temperate eucalypt woodlands that have been converted for cultivation and livestock grazing. While the superb parrot persists in these landscapes, the regeneration of the trees on which it depends for nest hollows has largely ceased because of suppression of tree regeneration by livestock grazing, cultivation, weeds and other human-induced disturbances (Fischer *et al*., 2009; Weinberg *et al*., 2011). Because mortality among existing trees is also high (Ozolins, Brack & Freudenberger, 2001), the number of trees with hollows is declining (Gibbons *et al*., 2008).

Study area

The study area is a major breeding area of the superb parrot, located on the south-west slopes of New South Wales (33°25′–35°18′S; 147°41′–149°24′E, *c*. 24 740 km^2; Manning *et al*., 2004). The vegetation type used by the superb parrot in this region is box-gum grassy woodland dominated by yellow box *Eucalyptus melliodora*, Blakely's red gum *E. blakelyi* and white box *E. albens*, often in conjunction with other species such as apple box *E. bridgesiana*, mealy bundy *E. nortonii*, red box *E. polyanthemos*, candlebark *E. rubida*, brittle gum *E. mannifera*, grey box *E. macrocarpa* and red stringy bark *E. macrorhyncha* (Benson, 1991, 1999; NSW NPWS, 2002). These woodlands once covered an extensive area of south-eastern Australia (Beadle, 1981; Department of Environment and Heritage, 2006). However, over 92% of woodland has been cleared, and what remains is highly modified (Threatened Species Scientific Committee, 2006), mostly consisting of small remnant patches and scattered paddock trees (Gibbons & Boak, 2002; Manning *et al*., 2004). Consequently, box-gum grassy woodlands are listed nationally as a critically endangered ecological community (Department of Environment and Heritage, 2006).

Predicting the availability of potential nest trees for the superb parrot

We used the simulation model described by Gibbons *et al*. (2008) populated with datasets from within our study area to predict the future availability of potential nest trees for the superb parrot under different conservation scenarios. This simulation model tracks the mean diameter at breast height (DBH) by size class and mean number of trees with hollows in stands through time with recruitment and mortality applied at pre-defined rates (Fig. 1). Parameters in the model (e.g. tree mortality) can be entered as random values within a range of observed or likely values so the predictions reflect the uncertainty of these parameters. The model is then run as many times as there are random values, so predictions for any single scenario are a summary of values from multiple runs of the model.

Data used to populate the simulation model

We calculated the mean number of trees in 10-cm DBH classes (i.e. 0–10 cm, 11–20 cm, etc.) for each tree species and health class (i.e. living or dead), based on data collected at 48 separate 2-ha sites in the agricultural matrix within our study area (the range of diameters recorded in the 48 × 2-ha sites for each species is provided in Supporting Information). To simulate tree growth over time, we developed a relationship between tree age and DBH using the following equation developed by Fischer *et al*. (2010):

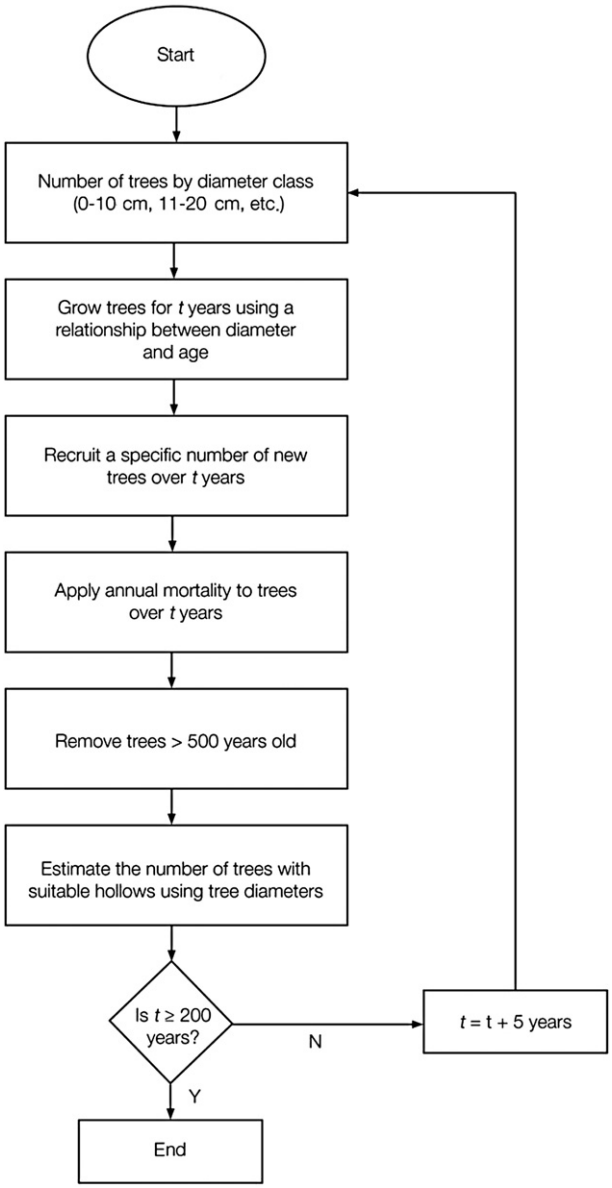

Figure 1 The process for modelling potential superb parrot *Polytelis swainsonii* nest trees.

$$Age = 0.02 \times \pi \times (DBH_{\text{standardized}}/2)^2 \quad (1)$$

where $DBH_{\text{standardized}}$ is the 'yellow box equivalent diameter' for each tree as defined in the following statements. Data on the relationship between age and DBH only exist for one tree species in our study area (yellow box) (Banks, 1997). To predict the ages of trees for other species, we followed the procedure outlined by Fischer *et al.* (2010), and calculated a 'yellow box equivalent diameter' for each individual tree of the other eucalypt species. The procedure assumed that all eucalypt species in our study area follow an identical growth curve relative to their maximum attainable diameter, and have the same approximate lifespan as yellow box. DBH values for all tree species were initially standardized as a proportion of the maximum attainable diameter for that species observed in the field (Supporting Information Table S1). Those values were then multiplied by the maximum diameter observed for yellow box (235 cm) to obtain a 'yellow box equivalent diameter'. We acknowledge that this procedure is unlikely to give precise age estimates, but it is a pragmatic solution given the paucity of data available for trees species in our study area.

The time-step in the simulation model was equivalent to the period between regeneration events (i.e. when new eucalypts become established). The mean age of trees in the smallest DBH classes (0–20 cm DBH) recorded at the 48 sites was *c.* 5–12 years. We used the most optimistic (shortest) period of 5 years between regeneration events in all scenarios representing business-as-usual (i.e. current management approaches continue into the future). For simulations representing business-as-usual [see scenario (a) in the following statements], we recruited trees at the mean [± standard error (SE)] rate of 0.02 ± 0.01 ha^{-1} for species group 1 (yellow box, Blakely's red gum) and 0.22 ± 0.18 ha^{-1} for species group 2 (white box, mealy bundy, apple box, red box), which is the mean (± SE) number of trees we recorded in the smallest DBH classes (0–20 cm DBH) at the 48 sites. A random value for the mean number of trees (per ha) recruited every time-step was selected from a normal distribution with a mean (± SE) equivalent to the estimates obtained for each tree species group to ensure that uncertainty in recruitment was reflected in our simulation modelling. Runs with negative values for recruitment were treated as zero recruitment. In an ideal situation, it may have been more appropriate to model recruitment stochastically given it may be, at least partly, an event-driven process. However, in the absence of data on the inter-annual variation of recruitment, we instead used mean data on recruitment over 5-year periods. We included two sources of mortality in our simulations. We calculated annual mortality from data collected on changes in the densities of scattered trees between 1964 and 1994 within the study area (Ozolins *et al.*, 2001). The mean (± SE) for annual mortality from this source was 0.013 ± 0.005. Gibbons *et al.* (2008) found that the numbers of scattered trees in these landscapes were highly sensitive to annual mortality, so for each run of the simulation model, we selected mean annual mortality randomly from a normal distribution with a mean ± SE of 0.013 ± 0.005 to ensure that uncertainty in mortality estimates was reflected in our simulation modelling. We also set, at 500, the maximum number of years that trees will remain living or standing, which is based on longevity estimates for yellow box reported by Banks (1997). There were no other data from which this estimate could be derived, and Gibbons *et al.* (2008) report that the number of scattered trees is not sensitive to this parameter in simulations of this type. As with recruitment, it may be more appropriate to model mortality stochastically, although data collected by Ozolins *et al.* (2001) over a period of 30 years did not indicate dramatic year-to-year variation in mortality,

perhaps because the principle driver of mortality in these modified landscapes is human-induced, and thus masks effects due to stochastic events such as climate or disease.

For the trees remaining at the end of each time-step, we predicted the proportion of trees that are potential nest trees for the superb parrot. Manning *et al*. (2004) observed that 98% of 136 nest hollows used by the superb parrot had a minimum entrance width of ≥ 5 cm, so we recorded a tree as a potential nest tree for the superb parrot if it contained ≥ 1 hollow with an estimated minimum entrance width of ≥ 5 cm. To predict potential nest trees, we recorded the presence/absence of hollows with minimum entrance width of ≥ 5 cm (hollows ≤ 1 m above the ground, in cut stumps and in fire scars at the base of trees were not included), DBH and tree species in all living and dead trees ≥ 5 cm DBH at 513, 50 × 20-m plots in our study region. In these 513 plots, we recorded 2665 living trees (Blakely's red gum, yellow box, white box, red box, mealy bundy and apple box) and 192 dead trees. We predicted the proportion of living trees that are potential nest trees for the superb parrot by fitting a generalized linear model with a logit link to these data in which the presence/absence of at least one hollow potentially suitable for the superb parrot in a tree (p_l) was the (binary) response variable, and DBH and tree species the explanatory variables. This model was:

$$Logit(p_l) = -4.11 + (0.07 \times DBH) - (2.38 \times \text{species group} = 2) \quad (2)$$

where species group was a factor with two levels (species group 1 is white box, red box, mealy bundy and apple box. Species group 2 is yellow box and Blakely's red gum). The relationships between DBH and the probability of hollows suitable for the superb parrot were not significantly different between the tree species in each group. The area under the receiver operating characteristic curve (AUC) for this model was 0.93, indicating the model had 'excellent' discriminating ability (Pearce & Ferrier, 2000). The model used for predicting the proportion of dead trees that are potential nest trees for the superb parrot (p_d) was

$$Logit(p_d) = -3.47 + (0.08 \times DBH) \quad (3)$$

The AUC for this model was 0.83, indicating the model had 'good' discriminating ability (Pearce & Ferrier, 2000).

Simulated scenarios

We simulated four alternative scenarios for conserving potential nest trees of the superb parrot. We use scenarios because they provide decision-makers with a broad range of management options to consider. Further, we know that persistence of tree hollows is most sensitive to mortality and recruitment (Gibbons *et al*., 2008), and different scenarios allow us to explore the effects of altering these key parameters. We include one scenario that is no further conservation action (1), and two based on the International Union for Conservation of Nature (IUCN) criteria for listing species [(b) and (c); IUCN, 2001]. We did this because (1) these scenarios relate to the percentage decline in a given population needed to meet the criteria for two IUCN status levels (critically endangered and endangered); (2) a link between superb parrots populations and nest hollow availability is likely in key parts of the landscape (i.e. scattered trees in the agricultural matrix) used for nesting within the study area (see Discussion section). The final scenario, scenario (d), relates to immediate conservation action to improve current levels of mortality and recruitment.

(a) No further conservation actions

Under this scenario, we commenced the simulation using current potential nest tree densities in the agricultural matrix (3.9 ha^{-1}), which is, conservatively, half of the mean density of potential nest trees that occurs in relatively unmodified remnants dominated by yellow box and Blakely's red gum (Gibbons *et al*., 2008). Current rural land management practices are assumed to continue, so no action is taken to increase existing tree landscape-scale tree recruitment or reduce existing tree mortality.

(b) Wait until 90% reduction in potential nest trees

We used the IUCN criterion of a 90% population decline (though not its rate) as a guide to trigger for conservation actions – this would equate to 'critically endangered' status if considering a species (IUCN, 2001). Under this scenario, we allowed potential nest tree density to drop to 0.8 ha^{-1} or *c*. 10% of pre-clearing levels, before landscape-scale tree recruitment at the rate of one new tree per ha planted every 10 years and reduction of annual tree mortality to half current levels.

(c) Wait until 70% reduction in potential nest trees

We used the IUCN criterion of a 70% reduction (although not the rate) as a guide to trigger conservation actions – this would equate to 'endangered' status if considering a species (IUCN, 2001). Under this scenario, we allowed the potential nest trees density to drop to *c*. 30% of pre-clearing levels (2.4 ha^{-1}), before there was landscape-scale tree recruitment at the rate of one new tree per ha planted every 10 years and reduction of annual tree mortality to half current levels.

(d) Implement enhanced conservation actions now

Under this scenario, we immediately implemented landscape-scale tree recruitment at the rate of one new tree per ha planted every 10 years and reduction of tree mortality to half current levels.

Scenario (a) represents the most likely (i.e. business-as-usual) scenario. Scenarios (b) and (c) were chosen to represent the implications of waiting until there are further reductions in populations of the superb parrot before trig-

gering a higher threat status and therefore increased conservation efforts. Scenario (d) represents the case where decline in potential nest trees to date triggers an immediate increase in conservation resources to redress the major factors causing the decline of potential nest trees. This is the least likely scenario.

Results

(a) No further conservation actions

Under this scenario, our modelling indicated that the density of potential nest trees would continue to decline from the current estimate of 3.9 ha^{-1}, which is *c.* 50% of the original (pre-clearing) estimate (8 ha^{-1}), over the 200-year simulation period (Fig. 2a). The predicted mean density of potential nest trees declined to 6% of the original (pre-clearing) estimate by the end of the simulation period (200 years).

(b) Wait until 90% reduction in potential nest trees

Under this scenario, we waited until a 90% decline in the density of potential nest trees relative to an original (pre-clearing) estimate (8 ha^{-1}) before implementing restoration actions. A predicted 90% decline in the mean density of potential nest trees relative to the original (pre-clearing) density occurred after 135 years. After initiation of restoration actions (reducing tree mortality and increasing tree recruitment), the predicted mean density of potential nest trees began to increase (Fig. 2b), but reached only 29% of the original (pre-clearing) mean density by the end of the simulation period (200 years).

(c) Wait until 70% reduction in potential nest trees

Under this scenario, we waited until a 70% decline in potential nest trees relative to the original (pre-clearing) estimate (8 ha^{-1}) before taking action. A predicted 70% decline in mean potential nest trees density relative to original (pre-clearing) density occurred after 40 years. After initiation of restoration actions (reduced tree mortality and increased tree recruitment), the predicted mean density of potential nest trees began to increase (Fig. 2c). By 200 years, the mean density of potential nest trees had reached 3.6 ha^{-1}, still below the current mean density, and 45% of the original (pre-clearing) mean density.

(d) Implement enhanced conservation actions now

Under this scenario, we immediately initiated restoration actions (reducing tree mortality and increasing tree recruitment). The predicted mean density of potential nest trees remained relatively stable over the simulation period. The predicted mean density of potential nest trees declined from the current mean density of 3.9 to 3.6 ha^{-1} at 60 years, before increasing to a mean of 4.1 ha^{-1} at the end of the simulation period (200 years), which is slightly above the current density (Fig. 2d).

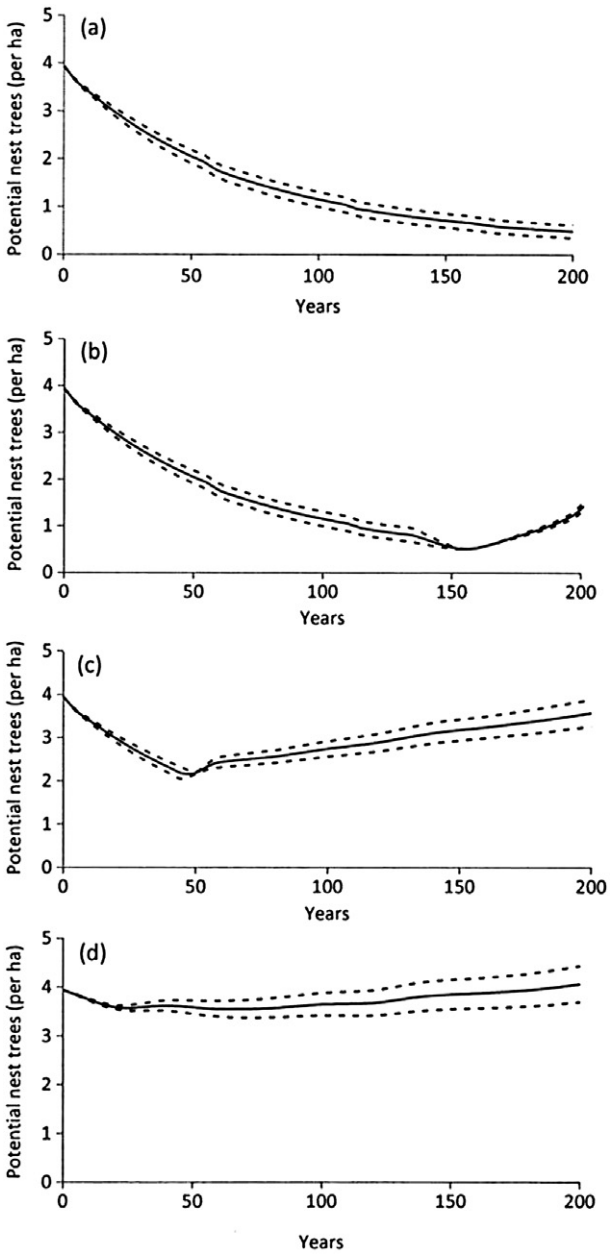

Figure 2 Predicted numbers (mean ± 95% prediction interval) of potential nest trees (per ha) for the superb parrot *Polytelis swainsonii* over 200 years under scenarios of (a) no further conservation actions (business-as-usual); (b) wait until 90% reduction in potential nest trees before implementing conservation actions; (c) wait until 70% reduction in potential nest trees before implementing conservation actions; and (d) implement enhanced conservation actions now.

Discussion

Conservation of hollow-dependent species in woodland and forest is a global issue (Saunders, Smith & Rowley, 1982; Newton, 1994, 1998; Gibbons & Lindenmayer, 2002; Lindenmayer *et al*., 2011). We have used one species, the superb parrot, to illustrate the universal problem of lag effects in managing potential nest trees of hollow-dependent species. To do this, we examined the effect of different conservation scenarios on potential nest trees for an obligate hollow-using species to illustrate the risk associated with lag effects. Our results demonstrate why it is essential to anticipate future hollow-limited bottlenecks as a result of long-term tree decline.

In three out of four scenarios [(a) to (c)], the number of potential nest trees was predicted to decline substantially. Even where a delayed response eventually took place [(b) and (c)], potential nest trees did not recover to current levels within 200 years. Under scenario (a) ('no further conservation action'), the potential for eventual local extinction of the superb parrot within the study area, as potential nest trees decline to very low densities, is evident. Although scenarios (b) and (c) did eventually begin to reverse the decline in potential nest trees, the risk is that society at that time may not choose, or be able, to act. Furthermore, if our predictions prove to be overly optimistic, e.g. because our models were too conservative (see Material and methods section), or if tree clearing accelerates (see following statements), the potential to act effectively in the future may be severely constrained. The only scenario that resulted in the predicted number of potential nest trees remaining stable over the next 200 years was scenario (d) ('implement enhanced conservation actions now'). This indicates that immediate action to reduce tree mortality and enhance tree regeneration within the study area will be essential to avoid serious impact on hollow availability for at least 200 years.

The mortality of scattered trees where they occur around the world is often increased by the intensification of agricultural production (Manning, Fischer & Lindenmayer, 2006*a*). For example, cultivated land expanded by 75% in our study area between the 1960s and 1990s (Ozolins *et al*., 2001). Global food demand is predicted to increase by 70–100% by 2050 (Godfray *et al*., 2010). In our study area, the growth of cultivated land is predicted to increase (Zhang *et al*. 2006; Blumenthal, 2010). In recent years, the majority of permits issued to clear native vegetation in this region have been associated with either converting pastoral land to cultivation, or introducing technologies (e.g. pivot irrigators, control-traffic farming) to increase productivity in cultivated land. Many of these applications can have a detrimental impact on the superb parrot. For example, in New South Wales, over a 3-year period from 2008 to 2011, 114 applications to clear native vegetation (including 85 applications to clear scattered paddock trees) had the superb parrot listed as likely to occur on the site. Of these, 49 applications were within our study area (NSW Office of Environment and Heritage, 2011). Our results clearly demonstrate that any actions that undermine or delay conservation efforts to reduce tree mortality and increased recruitment [i.e. scenario (d))] should be avoided.

Artificial nest boxes have been suggested as a possible approach to overcome hollow scarcity (McComb & Noble, 1981; Twedt & Henne-Kerr, 2001). However, recent monitoring of 3200 nest boxes placed along a major four-lane highway that crosses superb parrot breeding areas has not found a single breeding event in these artificial structures (D. Lindenmayer *et al*., unpubl. data). It is also not clear that nest boxes could be placed in sufficient numbers, at a landscape scale, and be maintained continuously for the 200+-year recovery periods indicated by this study. Current knowledge suggests that the maintenance and perpetuation of hollow-bearing trees is the most plausible solution for the conservation of the superb parrot.

In interpreting all scenarios, we assumed a positive relationship between the density of potential nest trees and populations of the superb parrot. This relationship is widely reported for hollow-dependent birds (Newton, 1994; Gibbons & Lindenmayer, 2002; Marsden & Pilgrim, 2003; Murphy, Legge & Heinsohn, 2003; Saunders *et al*., 2003; Heinsohn *et al*., 2009), and has been shown experimentally (Brawn & Balda, 1988; Aitken & Martin, 2008). However, the level at which hollow availability limits populations of the superb parrot is unknown. As with other hollow-dependent species, this will vary spatially, and in relation tree and hollow availability and competition from other species (Newton, 1998; Manning *et al*., 2004).

It has been postulated in a study of potential nest trees in roadside vegetation that hollows were unlikely to be limiting for the superb parrot (Davey & Purchase, 2004). It is highly unlikely such a conclusion (which was speculative only) could validly be extrapolated to the trees in the agricultural matrix that we modelled. This is because: (1) roadside vegetation is among the most undisturbed native vegetation in this part of Australia (Van der Ree & Bennett, 2001), and empirical research within the study areas has shown considerable differences in tree density between travelling stock reserves and adjacent paddocks (Lentini *et al*., 2011). Lentini *et al*. (2011, unpublished data) found that travelling stock reserves have on average 90.7 stems per ha (± 25.85), compared with 5.6 stems per ha (± 1.51) in adjacent paddocks. Furthermore, exotic 4.1 (± 1.49), wheat 2.2 (± 0.43), canola 1.6 (± 0.53) and Lucerne or clover paddocks 1.5 (± 0.37) had even fewer stems per ha. Because such land uses represent the majority in landscapes used by the superb parrots in the area we modelled, this has profound implications for the relative amount of hollows available (see later), and process-based prediction of population sustainability. (2) There is a greater level of threat (i.e. elevated level of mortality) from clearing, spray drift and fertilizers to trees in the agricultural matrix (Manning & Fischer, 2010) compared with trees in roadsides. (3) Roadsides represent a small proportion of the landscape compared with the agricultural matrix (the area we have modelled) where the majority of superb parrots occur (Manning *et al*., 2006*b*). Scattered tress and small remnants (< 1 ha) of the agricultural matrix represent 54% of the total area remaining of

this woodland (Gibbons & Boak, 2002). (4) Box-gum grassy woodland with very low tree densities (< 6 per stems ha over 15 cm DBH) has been shown empirically to support very low numbers of hollows potentially suitable for superb parrots (11 hollows over 5-cm diameter per ha) compared with low density (6–10 stems per ha and 31 hollows), medium density stands (11–50 stems and 74 hollows per ha) and high density (51–100 stems and 111 hollows per ha) (L. Rayner, unpubl. data). Low-density scattered trees are typical of the landscapes occupied by the superb parrot in the study area. Manning *et al.* (2004) found most (60%) of superb parrot nest trees in the study area were surrounded by only one to five trees within 50 m. Manning *et al.* (2006*b*) found most superb parrots occurred where there was low-density woodland. Therefore, we believe that it is reasonable to assume that as tree populations continue to decline in the agricultural matrix (as we have predicted), hollow availability will further limit the population size of the superb parrot (see Newton, 1994, 1998).

Critically, it is the inexorable trend observed in our modelling that should be of serious concern to conservation decision-makers. Failure to identify and respond appropriately to lag effects in restoration of nest hollows will place many dependent species at increased risk of extinction in the future. The predicted effects of lag times on tree hollow-dependent species are now beginning to be documented (e.g. Saunders *et al.*, 2003; Maron, 2005). Not only does waiting to act increase extinction risk and reduce future response options (Martin *et al.*, 2012), but it is also is likely to cost more (i.e. more trees will need to be regenerated) and will potentially be less successful because of synergistic processes affecting small populations, such as inbreeding and stochastic events (Lindenmayer & Fischer, 2006). Our novel application of an established modelling method provides an early warning approach that conservation managers can use to identify species at risk from longer-term ecological trends so that they can initiate vigorous conservation measures now. Without such approaches, there is a considerable risk that species facing future bottlenecks in key resources, such as those dependent on hollows, will always be disadvantaged by threat assessment processes (and derived policy and management actions) that (1) only consider short-term trends based on past and current population data and (2) do not identify and fully account for lag effects and longer-term trends in key resources and ecological processes.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1. Numbers of trees by diameter class for each tree species recorded in the study area.