



## How to make a common species rare: A case against conservation complacency

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### ABSTRACT

A traditional focus in conservation biology has been on rare species as they are often those most at risk of decline or extinction. However, we argue in this paper that some kinds of currently common species also can be susceptible to decline. Those at particular risk are species that are specialized on widespread environmental conditions. Such specialization may make such species vulnerable to a range of drivers of environmental change, placing them at risk of significant decline or even local extinction. We illustrate this with a case study of the arboreal marsupial the Greater Glider (*Petauroides volans*) in south-eastern Australia. The Greater Glider was formerly common in two large-scale studies but in one it suffered rapid extinction (within a 3 year period) and in another it is declining at an annual rate of 8.8%. We therefore argue for more research to better predict those kinds of currently common species which might be at risk of future rapid decline or extinction. In addition, we suggest there will often be a need to take pro-active conservation and management action to reduce the number of potential environmental stressors on populations of common species to ensure they do not become uncommon or rare. We also argue that conserving common species will ensure the retention of their key ecological and functional roles in ecosystems. Finally, we believe there is a need to develop better monitoring programs that can detect changes in the population trajectories of common species, help identify the reasons for temporal changes in such populations, and underpin timely management interventions. Despite these good intentions, we acknowledge that in one of our own long-term investigations we: (1) failed to anticipate the extremely rapid decline (and likely local extinction) of the Greater Glider, (2) were unable to diagnose the reason/s underpinning the population collapse, and (3) nor were we able to instigate a timely intervention program of management to prevent this from occurring. The key lesson from this sobering result is that common species can sometimes be at risk of rapid decline and it is wise to avoid complacency in conservation.

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### 1. Introduction

Conservation biology has long had a strong focus on rarity. There is now a large literature on the topic, including the various kinds of rarity that exist in nature (Cunningham and Lindenmayer, 2005; Gaston, 1994; Rabinowitz, 1981; Rabinowitz et al., 1986). There is also an extensive literature on the relationships between rarity, conservation status and the proneness of species to decline (Gaston, 1994; Koh et al., 2004; Lindenmayer and Fischer, 2006; O'Grady et al., 2004; reviewed by Gaston, 1994). Indeed, species are usually identified as 'at risk' only once they become rare (Gaston, 1994). However, if a key aim of conservation biology is to prevent species from declining or becoming extinct (Sodhi and Ehrlich, 2010; Soule, 1985), we ideally need to be pro-active and take steps toward early recognition and detection of threats, downward trajectories in abundance, and/or contracting distribution. As relatively simple as it may be to recognize rarity, it may not necessarily be an appro-

priate indicator of decline, particularly in the early stages of population decline (e.g. Caughley and Gunn, 1996; Cunningham and Olsen, 2009; Tilman et al., 1994). This is because some common species may be vulnerable to decline and/or eventual extinction (Gaston, 2010).

Species may be common for different reasons. They may be:

- Eruptive or cyclical and hence periodically common (e.g. Krebs et al., 2001; Robin et al., 2009).
- Generalists capable of exploiting a wide range of environmental conditions.
- Specialized on widespread environmental conditions.

We argue in this paper that species characterized by specialization on widespread environmental conditions may be particularly susceptible to environmental change, placing them at risk of significant decline or even local extinction. We believe this is a different kind vulnerability to decline or extinction than that of habitat and niche specialists which have previously been identified as being extinction prone (e.g. Breininger et al., 2006; Carlton et al., 1991;

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Colles et al., 2009; Johns and Skorupa, 1987; Koh et al., 2004; Lamberson et al., 1994; Sarre, 1995). We illustrate the risks of decline faced by common species that are specialized on widespread environmental conditions using a case example of an Australian arboreal marsupial, the Greater Glider (*Petauroides volans*), for which our major long-term research programs in south-eastern Australia have revealed broad-scale decline and/or susceptibility to environmental change. We discuss some of the key implications of our work for conservation programs. We argue that the conservation of common species is important for many reasons. These include:

1. Common species play particularly important roles in ecosystems including propagule dispersal, pollination, as well as comprising pivotal parts of food webs (Dickman and Steeves, 2004b; Gaston, 2010; Goldingay et al., 1991; Gregory et al., 2005; Sekercioglu, 2006).
2. Common species comprise the dominant structure and overall biomass in ecosystems (Gaston and Fuller, 2008; Gaston, 2010; Thompson, 2010) and contribute significantly to spatial and temporal variance in species richness patterns (e.g. Lennon et al., 2010; Vazquez and Gaston, 2004).
3. Common species may be those that are most likely to best adapt to rapid climate change (Steffen et al., 2009), may be those most useful as indicators of environmental change as well as biodiversity surrogates for other elements of the biota (Duelli and Obrist, 2003; McGeoch, 1998), and those most practical for some kinds of ecological monitoring (Devictor et al., 2007; McComb et al., 2010).

Given these important ecological, conservation and management roles, coupled with the fact that there are many examples of common and widespread species which have undergone a rapid decline or even extinction, we make a plea for more research to better predict those kinds of currently common species that might be at risk of decline or extinction in the future (e.g. Kotiaho et al., 2005).

## 2. Methods

### 2.1. Background – the ecology of the Greater Glider

The Greater Glider is a nocturnal arboreal marsupial with a distribution largely associated with eucalypt forests along the Great Dividing Range of eastern mainland Australia, from northern Queensland to southern Victoria (see Fig. 1). The species is the sole member of the genus *Petauroides* and the only gliding member of its family, the Pseudocheiridae. The Greater Glider is common and widespread and is generally thought to be the most secure species of marsupial glider in Australia apart from the Sugar Glider (*Petaurus breviceps*) (Clayton et al., 2006; Lindenmayer, 2002). However, at the same time, it is a species which has specialized on widespread environmental conditions through: (1) a specialized folivorous diet and a number of associated specialized physiological characteristics (Rubsamen et al., 1984; Youngentob et al., 2011), (2) a strong association with particular forest types (Braithwaite et al., 1984), and (3) a strong association with particular kinds of large trees that are used as nest and shelter sites (Gibbons and Lindenmayer, 2002). Below we further describe these aspects of the life history of the Greater Glider and how they may render the species susceptible to environmental change.

#### 2.1.1. Food requirements

The Greater Glider is folivorous and feeds almost exclusively on the leaves of eucalypt trees (Kavanagh and Lambert, 1990). The

species is totally absent from areas that lack eucalypt forest trees such as places that have been cleared and converted to stands of Radiata Pine (*Pinus radiata*) (Lindenmayer, 2009b). Adults of the Greater Glider weigh between 900 and 1700 g, although there is a smaller (600 g) northern subspecies (*P. volans minor*) confined to north of the Tropic of Capricorn in north Queensland (Comport et al., 1996; Lindenmayer, 2002). The body size of the Greater Glider is thought to be close to the smallest possible for a species totally dependent on foliage (Hume, 1999). Other species which rely primarily or exclusively on plant materials such as leaves tend to be characterized by a large body size to facilitate the intake of large quantities of comparatively nutrient-poor food and slow its passage through the gut (Hume, 1999). Two factors suggest that the Greater Glider is close to the limit of its energy budget: (1) the low nutrient content of its eucalypt leaf diet, and (2) the array of chemicals in eucalypt foliage which must be detoxified – a process which requires considerable energy and leads to large losses of nitrogen (Hume, 1999).

The concentrations of nutrients and herbivore-detering plant secondary metabolites (PSMs) in eucalypts often vary considerably from tree to tree, even within the same tree species and this creates a patchy distribution of forage quality across forest landscapes (Andrew et al., 2005; Wallis et al., 2002). A recent study by Youngentob et al. (2011) found that areas of the forest which contain low quality eucalypt trees in terms of nitrogen, available nitrogen, and particular eucalypt guild-specific PSMs (e.g. sideroxylonals) may not be able to sustain populations of the Greater Glider. Earlier research also found that the Greater Glider is most abundant in forest types that contain higher quantities of nitrogen and phosphorous (Braithwaite et al., 1984). Unlike the closely related Common Ringtail Possum (*Pseudocheirus peregrinus*) or Australia's other eucalypt folivore specialist, the Koala (*Phascolarctos cinereus*), the Greater Glider frequently consumes foliage from both major subgenera of eucalypts (*Eucalyptus* and *Symphymyrtus*). Since the Greater Glider regularly forages on both subgenera, it has to contend with a wide range of PSMs that can reduce the digestibility of plant nutrients and cause toxicosis. The reliance of the Greater Glider on nutritionally-poor foliage may make it particularly vulnerable to environmental changes that interfere with the ability of the species to access forage of suitable quality (e.g. habitat fragmentation (Youngentob et al., 2011)) or increase PSMs and decrease foliar nutrient availability (e.g. elevated atmospheric CO<sub>2</sub> associated with climate change (Kanowski, 2001)).

#### 2.1.2. Shelter requirements

The Greater Glider is an obligate cavity-dependent animal and trees with hollows are the only places the species can use for sheltering and nesting. Trees occupied by the Greater Glider are typically large diameter stems. This is because of the comparatively large body size of the species relative to other hollow-dependent mammals (Gibbons and Lindenmayer, 2002), but possibly also because of the insulative properties of large trees in regulating microclimatic conditions within cavities. This may be critical for the Greater Glider given its physiological intolerance to high temperatures (Rubsamen et al., 1984). Trees used as nest and den sites by the Greater Glider are typically tall. This is because tall trees provide points from which animals can readily volplane (up to 100 m) into the surrounding forest (Goldingay and Schiebe, 2000).

Consistent with the specialized den tree requirements of the Greater Glider, and coupled with the species' propensity to move frequently between many different trees within its home range (Kehl and Borsboom, 1984; Lindenmayer et al., 2004), the highest abundances of the species appear to occur in old growth forest stands where there are many large trees with hollows (Lindenmayer et al., 1995). Unlike several other species of arboreal marsupials, the Greater Glider exhibits limited flexibility in the kinds of trees it uses

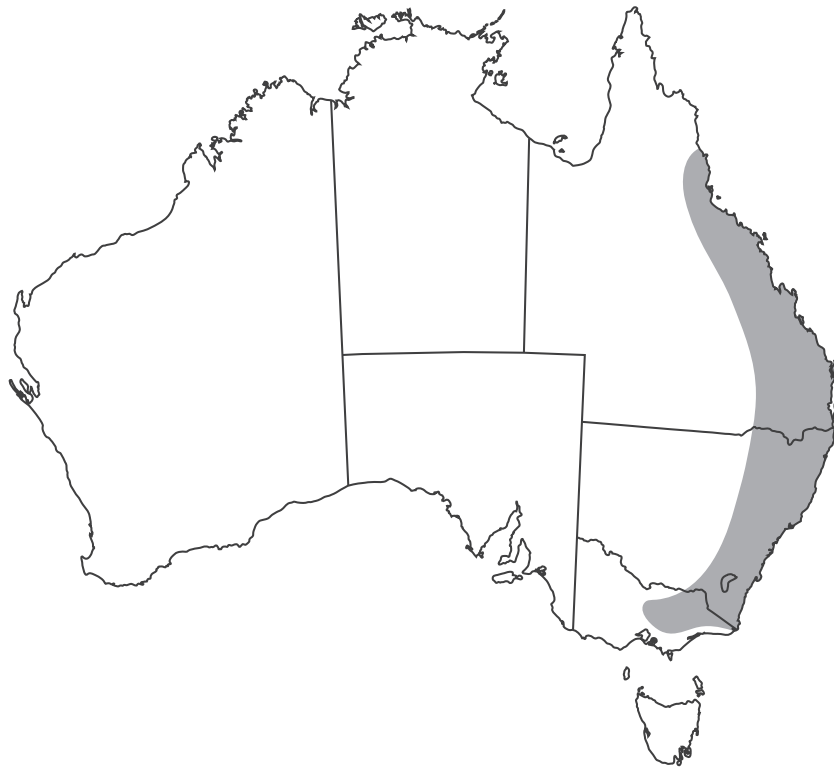


Fig. 1. Distribution of the Greater Glider.

as nest and den sites (Lindenmayer et al., in press). The Greater Glider is not known to use artificial nest sites such as nest boxes (Beyer and Goldingay, 2006; Lindenmayer et al., 2009b).

### 2.1.3. Habitat use, social behavior and reproductive system

The home range of the Greater Glider is about 1 ha (Henry, 1984; Pope et al., 2004) and the species is usually solitary except during the breeding season when pairs of animals are often recorded (Henry, 1984). Home ranges of males are generally exclusive, but those of males and females as well as neighboring females may overlap (Pope et al., 2004). The mating system of the species may vary between monogamy and polygamy depending on resource availability, although the species appears to be monogamous in most areas where it has been studied (Lindenmayer, 2002). The sex ratio in populations of the Greater Glider varies between a female bias of 1:1.5 (Tyndale-Biscoe and Smith, 1969a) and parity (Norton, 1988). One offspring may be produced annually. However, up to 50% of females do not breed in any given year and juvenile mortality may exceed ~20% in any given year (Tyndale-Biscoe and Smith, 1969a). Young of the Greater Glider spend 6 months in the pouch followed by 4 months as dependent nestlings. Animals then disperse at 1 year of age with adult males enforcing the dispersal of sub-adult male conspecifics which results in substantial male-biased mortality (Tyndale-Biscoe and Smith, 1969a). The Greater Glider reaches sexual maturity at 2 years of age and the maximum lifespan is probably 10–12 years (Tyndale-Biscoe, 2005).

A number of studies indicate that the Greater Glider may have a somewhat limited dispersal capability. Suckling (1982) suggested the dense tree cover of plantation trees may impede the movement of the species through plantation landscapes. This is congruent with work by Taylor et al. (2007) which uncovered genetic evidence of impaired dispersal among populations of the Greater Glider between patches of remnant eucalypt forest surrounded by stands of plantation Radiata Pine.

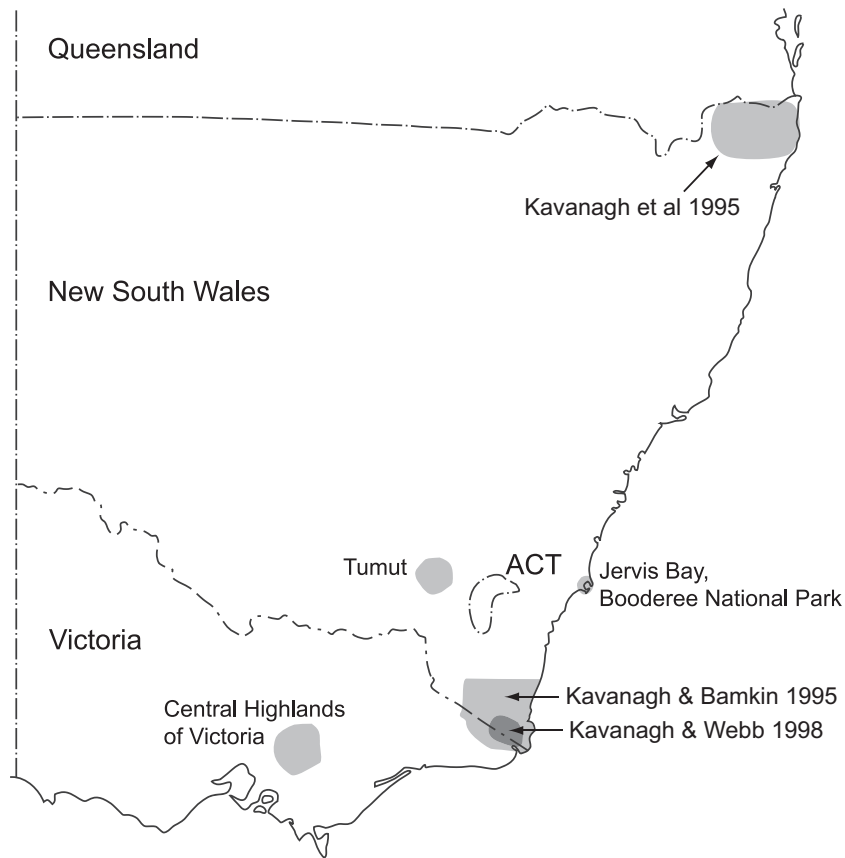
In summary, while there are numerous definitions of specialization in the ecological literature (reviewed by Colles et al., 2009; Devictor et al., 2010) and it seems to be re-defined for almost each new publication on the topic, the Greater Glider is not specialized in the most widely recognized sense in that it has a large distribution covering several thousand kilometers along the east coast of mainland Australia (Fig. 1). Moreover, it occupies a wide range of forest types spanning an elevational gradient from sea level to 1400 m and the species can be locally abundant in suitable habitat. However, within the broad-scale distributional limits of the Greater Glider, individuals of the species are typically most likely to occupy stands of old forest with the largest diameter and tallest trees. They also are most likely to feed in trees with high levels of foliage nutrients but low levels of toxic secondary compounds. Thus, specialization is not on forest type, but rather on vegetation structure and leaf chemistry.

## 2.2. Case study of the Greater Glider

Our case study is based on data from 436 long-established field sites that comprise three large-scale, long-term empirical studies (Fig. 2). The sites encompass native forests in large reserves and wood production (logged) forests, as well as remnant patches of eucalypt forest within an exotic Radiata Pine plantation. The sites in these large-scale studies vary in natural disturbance regimes (e.g. wildfire) as well as the extent of human disturbance in the surrounding landscape (e.g. native forest logging vs plantation logging vs no harvesting).

### 2.2.1. Victorian Central Highlands study

This study includes 160 permanent 1 ha sites located across a 180 000 ha area in the montane ash forests of the Central Highlands of Victoria. There are 81 sites in the Yarra Ranges National Park, with the remaining sites in forests broadly designated for wood production. Notably, 64 of the 160 sites were burned in



**Fig. 2.** The general location of large-scale, long-term empirical studies in south-eastern Australia. The locations of other major studies of the Greater Glider by Kavanagh and Bamkin (1995), Kavanagh et al. (1995), and Kavanagh and Webb (1998) are also shown.

the 2009 Victorian wildfires. The 160 sites vary in forest age class (20–300+ years old), number of trees with hollows, slope, aspect, and a range of other variables (Lindenmayer, 2009a).

These sites have been monitored annually for the Greater Glider between 1997 and 2010 (Lindenmayer, 2009a). Surveys of arboreal marsupials in the Central Highlands of Victoria are based on the stagwatching method, in which all large trees with hollows on given sites are watched simultaneously around dusk by trained observers to provide a count of all animals emerging from their nest sites (Lindenmayer, 2009a).

#### 2.2.2. Jervis Bay study

Our second empirical study is from the 6500 ha Booderee National Park in the Jervis Bay Territory on the south coast of New South Wales. Booderee National Park has full protected area status in which vegetation clearing, urban development, logging and plantation establishment are excluded. Our work has entailed repeated annual spotlighting counts of the Greater Glider between 2003 and 2009 on 110 permanent 1 ha sites located throughout Booderee National Park. These sites are stratified across different vegetation types (rainforest, forest, woodland, shrubland, heathland and sedgeland) and burning history classes (0–5 past fires) (see (Lindenmayer et al., 2008)). Fifty-two of our 110 field sites were burned in a major wildfire in late 2003.

#### 2.2.3. Tumut fragmentation study

Our third empirical study is from the Tumut region of New South Wales, south-eastern Australia. Work on the Greater Glider in the region has entailed spotlighting surveys in 1996 and 2007 at 166 permanent field sites, each 600 m long and 100 m wide. The 166 sites comprised 40 sites in large contiguous areas of native eucalypt for-

est, 86 patches of remnant eucalypt forest surrounded by extensive stands of exotic Radiata Pine plantation, and 40 sites dominated by Radiata Pine trees (Lindenmayer, 2009b). The 86 eucalypt remnants encompassed four patch size classes (1–124 ha), two patch shapes (elongated and elliptical), five forest types, and two time-since-establishment classes (Lindenmayer, 2009b). In the period between the 1996 and 2007 surveys of the Greater Glider, there had been considerable landscape change resulting from harvesting and replanting activities in the pine plantations which surrounded the eucalypt remnants in the study region at Tumut.

#### 2.2.4. Statistical analyses

The new results reported in this paper were obtained by fitting Hierarchical Generalized Linear Models (HGLMs) (Lee et al., 2006) to our major datasets. Further details of earlier results summarized in this paper are given in Lindenmayer (2009a,b) and Lindenmayer et al. (in press).

### 3. Results

#### 3.1. Victorian Central Highlands study

The Greater Glider was a commonly recorded species at the commencement of our monitoring program in 1997 and was detected on 42 of the 160 monitoring sites at that time. The species declined significantly during the 12 years of study to 2010 (Wald Statistic,  $\chi^2_1 = 7.1$ ,  $P = 0.008$ ) (Fig. 3). The estimated annual rate of decline of the Greater Glider was 8.8% (95% confidence interval = 2.2–15.8%). This temporal trend could, in part, be explained by rainfall, with a significant negative relationship between the

abundance of the species in a given year and rainfall two winters previously (Wald statistic,  $\chi^2_1 = 23.2$ ,  $P < 0.001$ ). We also found that the probability of observing the Greater Glider was significantly ( $\chi^2 = 9.40$ , d.f. = 1,  $P = 0.002$ ) higher on our sites located in the Yarra Ranges National Park than in forests broadly designated for pulp and timber production. We identified a significant positive relationship between the abundance of the Greater Glider and both the age of the forest and the numbers of trees with hollows on a site (Wald statistic,  $\chi^2_1 = 4.3$ ,  $P = 0.039$ ). Finally, the Greater Glider was not recorded in spotlighting surveys of any of our field sites that were burned in 2009 by a major wildfire.

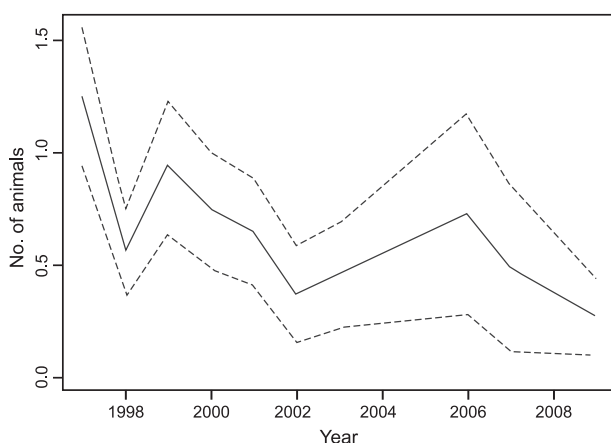
In summary, our data for the Greater Glider in Victoria suggest that the species is sensitive to several key factors including: (1) Declining rainfall over the past decade (see Cai and Cowan, 2008). (2) Forest landscape change – as reflected by differences in the occurrence of the species between in the Yarra Ranges National Park and wood production forests. (3) Clear-cut logging, as indicated by both the absence of the species in forests that have been logged and regenerated in the past 35 years (Lindenmayer, 2009a) and relationships between the occurrence of the species and the significant reduction in abundance of large trees with hollows which are traditionally removed by timber harvesting operations (Lindenmayer et al., in press). And (4) Wildfire, as indicated by lack of detections of the species in any sites burned in 2009 (Lindenmayer et al., unpublished data).

### 3.2. Jervis Bay study

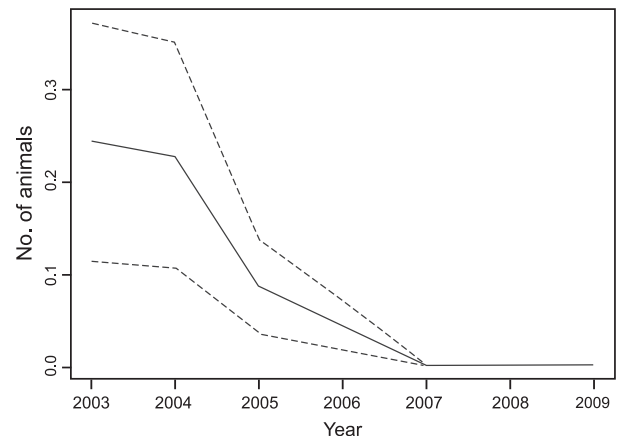
In 2002, the Greater Glider was recorded at 22 of our 110 field sites in Booderee National Park. It was the second most commonly detected arboreal marsupial (after the Common Ringtail Possum) at that time. The Greater Glider was found to be significantly more likely to occur in rainforest and eucalypt forest than other vegetation types (e.g. woodland, heathland and shrubland) ( $P = 0.004$ ) (Lindenmayer et al., 2008). Since 2004, the Greater Glider has declined significantly across all vegetation types in Booderee National Park ( $P < 0.001$ ) and has not been recorded in any of our (three) repeated spotlighting surveys since 2007 (Fig. 4). It is quite possibly now extinct in the study area.

### 3.3. Tumut fragmentation study

Extensive surveys at Tumut in 1996 (Lindenmayer et al., 2009b) and repeated in 2007 (Youngentob et al., unpublished data) con-



**Fig. 3.** Temporal changes in the mean numbers of the Greater Glider per 1 ha field site within the ash-type eucalypt forests of the Central Highlands of Victoria, south-eastern Australia. The solid black line corresponds to the mean response and the hatched lines are the 95% confidence intervals for the mean response.



**Fig. 4.** Temporal changes in the mean numbers of the Greater Glider per 1 ha field site in Booderee National Park, south-eastern Australia. The solid black line corresponds to the mean response and the hatched lines are the 95% confidence intervals for the mean response.

firmed the results of earlier work by Tyndale-Biscoe and Smith (1969b) that the Greater Glider does not inhabit stands of Radiata Pine plantation that were formerly native forest and previously supported the species (Lindenmayer, 2009b).

The work at Tumut also has demonstrated that the Greater Glider responds strongly to landscape context and other related kinds of effects. We have found that the species is significantly less likely to occur in remnant eucalypt patches surrounded by Radiata Pine stands than in contiguous eucalypt forest ( $\chi^2_1 = 13.43$ ,  $P < 0.001$ ) (Lindenmayer et al., 1999). In addition, the Greater Glider is significantly less abundant in remnant eucalypt patches surrounded by Radiata Pine stands than in contiguous eucalypt forest ( $F_{1,93} = 16.05$ ,  $P < 0.001$ ) (Lindenmayer et al., 1999; Youngentob et al., unpublished data). The probability of occurrence of the Greater Glider is also significantly lower in: (1) small eucalypt remnants ( $P < 0.001$ ), and (2) eucalypt remnants dominated by Broad-leaved Peppermint (*Eucalyptus dives*), Apple Box (*Eucalyptus bridgesiana*), Red Stringybark (*Eucalyptus macrorhyncha*), Swamp Gum (*Eucalyptus camphora*), Black Sallee (*Eucalyptus stellulata*), or Snow Gum (*Eucalyptus pauciflora*). Indeed, the Greater Glider was recorded commonly in only those eucalypt patches dominated by Narrow-leaved Peppermint (*Eucalyptus radiata*) or Ribbon Gum (*Eucalyptus viminalis*) (Lindenmayer, 2009b; Lindenmayer et al., 1999). In more recent studies, Youngentob et al. (unpublished data) found that the probability of occurrence of the Greater Glider is significantly lower in eucalypt patches where the surrounding Radiata Pine stands have been clear-cut and then replanted since 1996 ( $\chi^2_1 = 3.51$ ,  $P = 0.061$ ) and this effect is strongest in small eucalypt remnants ( $\chi^2_1 = 5.18$ ,  $P = 0.023$  and  $F_{1,58} = 17.97$ ,  $P < 0.001$  for presence and abundance respectively). Finally, populations of the Greater Glider exhibited significantly reduced levels of genetic variation associated with demographic isolation within eucalypt remnants separated by stands of Radiata Pine (Taylor et al., 2007).

In summary, our data for the Greater Glider at Tumut indicate the species responds negatively to a number of environmental factors. These include landscape context and fragmentation effects as revealed by: (1) Differences in animal presence and abundance between sites in contiguous areas of native eucalypt forest and sites in eucalypt remnants surrounded by stands of Radiata Pine (Lindenmayer, 2009b). (2) Reduced occupancy and abundance in small eucalypt remnants that had experienced recent disturbance to the adjacent Radiata Pine matrix (Lindenmayer, 2009b; Youngentob et al., unpublished data). And (3) Reduced levels of genetic variation within eucalypt remnants (Taylor et al., 2007). The Greater

Gliders are also sensitive to forest clearing as suggested by the total absence of the species from the extensive stands of Radiata Pine that have been established on areas that were formerly native forest and known to be previously inhabited by large populations of the species (Lindenmayer, 2009b; Tyndale-Biscoe and Smith, 1969b).

#### 4. Discussion

Our work on the Greater Glider suggests that some kinds of common and widespread species that are specialized on prevailing widespread environmental conditions may be at risk of rapid (and sometimes highly significant) decline when environmental conditions change. Specialization on widespread environmental conditions may mean such species are susceptible to the effects of one or more potential threatening processes as illustrated in our case study (see Table 1). For example, the forests in our various study regions have been influenced by a variety of factors and types of disturbance such as (1) plantation establishment, harvesting and then re-establishment, (2) native forest logging, and (3) wildfire. In addition, south-eastern Australia has been subject to prolonged periods of extreme temperature and below average rainfall during the past decade (Cai and Cowan, 2008). The factors associated with the temporal changes which we documented for the Greater Glider appeared to vary between study regions, although we are acutely aware that not all factors are equally applicable or have been equivalently studied in all regions (Table 1). For example, the decline of the Greater Glider in the ash-type forests of Victoria appears to be related, in part, to its extreme selectivity for particular kinds of trees with hollows and, in turn, the significant depletion in the availability of these key denning and nesting resources by traditional forms of clear-cut logging. Extreme selection of particular kinds of food resources and impaired dispersal across the Radiata Pine-dominated landscape matrix may have underpinned the highly significant landscape context and related effects on the Greater Glider that we recorded at Tumut. A paucity of sufficient suitable den trees within small patches of remnant eucalypt forest (Lindenmayer et al., 2004) also may have contributed to the landscape context effects we have quantified for the Greater Glider at Tumut.

The underlying reasons for the dramatic decline in populations of the Greater Glider in Booderee National Park (Fig. 4) remain elusive. They cannot be attributed to the *direct* effects of the major and widespread fire which occurred in Booderee National Park in 2003 or to rainfall. The decline is also not associated with logging or habitat fragmentation. It is possible that the Greater Glider is in an extinction debt (sensu Tilman et al., 1994) resulting from activities like urbanization which may have blocked the peninsula to immigration by animals from other forested environments outside Booderee National Park. This is thought to have occurred in the sin-

gle, small population of the Yellow-bellied Glider (*Petaurus australis*) in Booderee National Park in the mid-1980s. However, our spotlighting surveys suggest that, unlike the Yellow-bellied Glider, the Greater Glider seems to have declined from many small sub-populations scattered across the entire reserve. Such a rapid decline would not therefore appear to be consistent with an extinction debt. Notably, there appears to be no evidence of an extinction debt in the Greater Glider in the Tumut Fragmentation in which animals have occupied numerous small patches of remnant eucalypt forest surrounded by stands of plantation pine for more than 10 years and possibly 70 years (Lindenmayer, 2009b).

One possible, but also highly unanticipated, explanation for the dramatic collapse of populations of the Greater Glider at Booderee National Park is altered trophic interactions due to the control of exotic predators and subsequent increasing predation pressure from wide-ranging forest owls. Large forest owls and, in particular, the Powerful Owl (*Ninox strenua*) are common in Booderee National Park (Debus, 1997) and detections of them have more than doubled from 30.9% of sites in 2003 to 67.2% of sites in 2009 (Lindenmayer et al. unpublished data). In addition, in the past 4 years, we have confirmed the first records of the Sooty Owl (*Tyto tenebricosa*) in Booderee National Park. At the same time, populations of other predators like the introduced Red Fox (*Vulpes vulpes*) have been reduced through a co-ordinated poison baiting program that commenced prior to the establishment of our research program in Booderee National Park (Roberts et al., 2006). The Red Fox rarely preys on canopy dwelling animals like the Greater Glider. However, it is known to consume many other species of animals in Booderee National Park (Roberts et al., 2006) that are also taken by the Powerful Owl and the Sooty Owl (Debus et al., 2009). Thus, it is possible that a reduction in the abundance of the Red Fox may have released competition for prey with the Powerful Owl and the Sooty Owl with corresponding changes in owl populations then having negative impacts on populations of the Greater Glider. The most obvious management intervention would therefore be to shoot large forest owls. However, the conservation dilemma here is that the Powerful Owl, Sooty Owl and Masked Owl are all threatened species and therefore killing them is simply not a practical management option.

It is distinctly possible that some of the key factors influencing populations of Greater Glider in the different study regions may have cumulative and/or synergistic effects. For example, forest clearing in the Tumut region is known to remove trees with hollows used by the Greater Glider, leading to a direct increase in the levels of mortality. It also increases the hunting efficiency of predators of the Greater Glider (Tyndale-Biscoe and Smith, 1969b). In the wet forests of Victoria, there may be complex interactive effects of logging and fire in which harvested and regenerated stands become highly fire-prone and are likely to re-burn at an increased frequency and severity compared with unlogged areas (Lindenmayer et al., 2009a). The traditional green forest log-

**Table 1**  
Response of the Greater Glider to potential threatening processes in different study regions.

Location	Rainfall	Fire	Fragmentation	Logging	Loss of, or limited number of, tree hollows
Victoria	Yes	Yes	Possible <sup>a</sup>	Yes	Yes
Booderee National Park	No	No	Possible <sup>b</sup>	N.A.	N.A.
Tumut	Not tested <sup>c</sup>	N.A.	Yes <sup>d</sup>	Yes <sup>d</sup>	Yes <sup>e</sup>

<sup>a</sup> Possible as reflected by significant forest tenure effects. In areas used for forest harvesting, connectivity in surrounding habitat can be reduced by clear-cut logging.

<sup>b</sup> Possible as Booderee National Park is a peninsula with significant urban development at its distal end. Given the limited dispersal ability of the Greater Glider (Taylor et al., 2007), opportunities for the reversal of this apparent localized extinction may be scant.

<sup>c</sup> Not appropriate to be tested because datasets comprise two points in time (1996 and 2007).

<sup>d</sup> Manifested through landscape context effects via logging of Radiata Pine stands surrounding eucalypt remnants.

<sup>e</sup> Indicated by significant changes in den tree use in small eucalypt remnants that support few trees with hollows (Lindenmayer et al., 2004; Pope et al., 2004) and increased competitive pressure for hollows between the Greater Glider and the larger Common Brushtail Possum (*Trichosurus vulpecula*) in small and linear eucalypt patches (Youngtob et al., unpublished data).

ging, fire, or post-fire salvage logging individually would have negative impacts on populations of the Greater Glider, but in combination these drivers could be a significant contributor to the decline of the species.

Finally, long-term work in each of our three empirical studies has encompassed not only populations of the Greater Glider but populations of arboreal marsupials *per se*. Some of the drivers of population decline in the Greater Glider (see Table 1) also have a negative effect on other species of arboreal marsupials. The loss of trees with hollows through native forest logging, changes in landscape context associated with plantation establishment and harvesting, and wildfire are prominent examples (Lindenmayer, 2009a,b). However, we note that in each of the regions where we have conducted long-term studies of arboreal marsupials, the Greater Glider has been: (1) the only species of arboreal marsupial to exhibit a marked and highly significant decline (Victoria) (Lindenmayer et al., in press), (2) the species of arboreal marsupial exhibiting the most marked decline (Booderee National Park) (Lindenmayer et al., 2008), or (3) the species of arboreal marsupial most significantly affected by landscape change (Tumut) (Lindenmayer, 2009b; Lindenmayer et al., 1999).

#### 4.1. Other studies of the Greater Glider

Studies elsewhere in south-eastern Australia by other workers also have indicated that the Greater Glider is highly sensitive to environmental changes. For example, Kavanagh and Webb (1998) (see Fig. 2) studied a 500 ha area of wood production forest near Bombala in southern New South Wales in south-eastern Australia and found that the Greater Glider was the species of arboreal marsupial most sensitive to logging. The Greater Glider declined on all logging compartments and had not recovered 8 years after harvesting (Kavanagh and Webb, 1998). A more broadly based study of fauna on 200 field sites located throughout a ~100 km × 60 km area of southern New South Wales also showed that the occurrence of the Greater Glider was strongly associated with unlogged forest (Kavanagh and Bamkin, 1995). A similarly large-scale study on the north coast of New South Wales likewise identified the Greater Glider as the vertebrate species most sensitive to intensive logging operations (Kavanagh et al., 1995).

#### 4.2. Implications for conservation

We believe that our work has some critically important implications for conservation and natural resource management. First, there may be cases where it is problematic to use rarity as a surrogate for decline or extinction risk. Indeed, as illustrated in our case study, some initially common species may be at risk of rapid decline (e.g. see Fig. 4). Thus, while there is considerable conservation biology literature focused on the plight of rare and endangered species, we suggest there is also a need to ensure the conservation of some kinds of (presently) common species, but which are at risk of decline. Indeed, the ecological and conservation literatures contain many examples of formerly common and widespread species which have declined rapidly and/or eventually become extinct. Classic cases include the Passenger Pigeon (*Ectopistes simigra*) and Rocky Mountain Grasshopper (*Melanoplus spretus*), both initially extremely abundant species but which are now long extinct (Chapco and Litzenger, 2004; Gurney and Brooks, 1959; Schorger, 1973). Similar examples from North America include those of Regal Fritillary (*Speyeria idalia*) which has lost from almost all of its distribution east of the state of Indiana in the USA (Powell et al., 2007) and a range of species of bumblebees (Cameron et al., 2011). The Silversword (*Argyroxiphium sandwicense*) from the Hawaiian islands was once so abundant that individual plants were dislodged and rolled away for sport (Kimura and Nagata, 1980), but

this iconic plant species is now highly endangered. The common and widespread Woodland Caribou (*Rangifer tarandus caribou*) has declined substantially throughout North America since the 19th century (Faille et al., 2010). Australia supported a wide range of native mammal species that were once widespread and abundant (Bilney et al., 2009), a number of which are now either extinct or are rare and occupy less than 1–5% of their former range (Dickman, 2007). Many species of common and widespread birds have declined in agricultural areas in Europe (Krebs et al., 1999) and these include well known taxa like the Common Starling (*Sturnus vulgaris*) and the House Sparrow (*Passer domesticus*) in the United Kingdom (Freeman et al., 2008; Vincent, 2005). Elliott et al. (2010) have recently documented the long-term decline of common and widespread birds in low elevation areas of the North Island of New Zealand. Similarly, a large number of common and widespread butterflies have declined dramatically following intensive human use of landscapes (Van Dyck et al., 2009), as is also the case for a very large number of species targeted by commercial fishing (Levin et al., 2006).

Given this record of rapid decline of common and widespread species, a key question arises: Is it possible to identify and/or predict currently common species that are potentially at risk? Based on a detailed analysis of Finnish butterflies, Kotiaho et al. (2005) suggested that species which are not listed as threatened but which share many characteristics with threatened species should have their status re-considered. This is a useful approach but we suggest that, based on our findings, there also would be value in identifying other species like the Greater Glider which are specialized on widespread environmental conditions and may be at risk of decline when environmental conditions change. As we discuss further below, such efforts would need to be coupled with high quality longitudinal data to determine the actual population trajectories of species thought to be at risk.

A second important implication of our work is that there often will be a need to take pro-active action to reduce the number of potential environmental stressors on populations of common species. This is critically important: many studies have demonstrated that significant decline and/or extinction is frequently the result of multiple threatening processes (Caughley and Gunn, 1996; Lindenmayer and Burgman, 2005; Simberloff, 1988). In the case of populations of the Greater Glider in the wet forests of Victoria, this means limiting the amount of clear-cut logging. This is because such operations reduce the abundance of the key types of large diameter, tall trees (Lindenmayer et al., 1991) on which the species depends, and create the logged sites and logged landscapes where the species is significantly less likely to occur. In the plantation-dominated landscapes at Tumut, mitigating logging effects on the Greater Glider will entail staggering the timing of harvesting operations in the Radiata Pine stands which surround patches of remnant native forest. This ensures that remnant patches of native forest are bordered by a mixture of mature and regenerating pine stands and not uniform areas of recently clear-cut plantation. These steps in both systems are critically important to instigate as soon as possible given the potential for very rapid decline as illustrated by our work at Booderee National Park (see Fig. 4).

A third important implication of our work is the need for greater recognition by conservation biologists and environmental policy makers of the reasons to go beyond the traditional focus on endangered species and to take steps to conserve some kinds of common species and ensure they do not become uncommon or rare. Conserving common species also ensures they maintain their key ecological and functional roles in ecosystems (Dickman and Steeves, 2004a; Gaston, 2010), thereby avoiding other problems such as disruption of mutualistic relationships. In the case of the Greater Glider, the species is an important part of forest food webs and is known to be a key prey item of large forest owls of conservation concern like

the Powerful Owl (Kavanagh, 1988) and Sooty Owl (Debus et al., 2009). In addition, early instigation of conservation action before common species undergo serious decline may be more effective than actions undertaken when a species is uncommon or rare. For example, “crisis management” strategies like captive breeding and reintroduction programs have a high risk of failure (Fischer and Lindenmayer, 2000). In the particular case of the Greater Glider, the species has bred very poorly in captivity (Jackson, 2003), translocations of it have been spectacularly unsuccessful (Tyndale-Biscoe and Smith, 1969b), and there has been no successful reintroduction program published to date (Sheean et al., in press).

Finally, our work highlights the importance of long-term data for rigorously quantifying population trajectories. High quality empirical data for common species may often be easier to gather than for uncommon or rare species. In the case of our long-term work in Victoria, it was possible to gather far better empirical data on the Greater Glider than less common but higher profile species like the nationally endangered Leadbeater’s Possum (*Gymnobelidues leadbeateri*) and vulnerable Yellow-bellied Glider (Lindenmayer, 2009a; Lindenmayer et al., 2003). Well designed and executed monitoring programs of common species have the potential to help identify the reasons for temporal changes in populations in a timely way so that interventions can be implemented to halt population declines before they are difficult to reverse – key elements in effective conservation (Caughley and Gunn, 1996; Lindenmayer and Likens, 2010; McComb et al., 2010). However, we are acutely aware that despite our carefully designed monitoring program in Booderee National Park, we nevertheless failed to anticipate the extremely rapid decline (and possible local extinction) of the Greater Glider. In addition, despite ruling out some factors as direct drivers of decline (e.g. wildfire, reduced rainfall, landscape fragmentation and logging), we were unable to diagnose the reason/s underpinning the population collapse in Booderee National Park. Thus, we were unable to instigate a targeted intervention program of management to arrest its decline and possible extinction. This sobering result emphasizes two key points: First, biodiversity monitoring programs need to be carefully designed to ensure the early detection of changes in population trajectories and avoid ‘unpleasant’ ecological surprises (Lindenmayer et al., 2010; Wintle et al., 2010). Second, that as common species can sometimes be at risk of rapid decline, complacency in conservation is unwise.

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