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Population structures of the widespread Australian conifer *Callitris columellaris* are a bio-indicator of continental environmental change

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ABSTRACT

Massive environmental changes have occurred since European settlement of Australia more than 200 years ago. We examined the demographics of *Callitris columellaris* F. Muell. (Cupressaceae) across Australia as a potential bio-indicator of environmental change. This species is a widespread obligate seeder with large reproductive potential but is sensitive to fire and herbivory. We measured variation in tree size, stem density, basal area, and seedling recruitment among 90 sites that encompassed a wide range of climates and landscape settings across Australia. Soils from each site were analysed for pH, %C, % N and %P. We also noted evidence of fire and herbivory. Climate at each site was classified as tropical, temperate or arid. Case studies and published literature are used to illustrate the contrasting effects of disturbance in the three climate zones. Climate had a strong influence on stand basal area, density of juveniles and proportions of seedlings and saplings in a population, as well as on prevailing disturbance regimes. Structure of *Callitris* populations was not strongly associated with soil fertility. In the arid zone overall, and in many individual populations, there were relatively few juveniles and evidence of a chronic recruitment deficit during the last 100–200 years, consistent with reported adverse effects of introduced herbivores on *Callitris* regeneration. By contrast, most tropical and temperate populations conformed to a negative exponential distribution, consistent with frequent regeneration. Many temperate sites showed extremely dense juvenile populations. In the tropics, juvenile density is lower, probably because of frequent, relatively mild fires that kill many juveniles but few adult trees. We conclude that *C. columellaris* is a sensitive bio-indicator, and is in decline across much of arid Australia, reflecting the inherent vulnerability of ecosystems in regions with low productivity.

1. Introduction

Australia has experienced massive environmental change in the two centuries since European settlement. For example, extensive land clearing, introduction of exotic plants and animals, widespread provision of artificial watering points and the breakdown of Aboriginal land management have contributed to the worst record of mammal extinctions of any continent (McKenzie et al., 2007) and major declines in long-lived plant species (Auld and Keith, 2009). Given that much of the native vegetation remains uncleared and it is still possible to analyse the vegetation patterns that existed prior to European colonisation, we suggest that continent-wide surveys of the demographic status of widespread, long-lived tree species can provide a valuable perspective on the environmental changes that have occurred during this time. For example, in the arid zone, current size distributions of many long-lived plant species are heavily skewed, with few or no juvenile or young adult plants present because new recruits do not persist under the current grazing regime (Auld and Keith, 2009). Thus presence of juveniles of these species is a particularly sensitive index of ecosystem health. In addition, analysis of population size class structures can add temporal depth to a spatial survey of tree recruitment and indicate whether tree populations are stable (Rubin et al., 2006; Drewa et al., 2008). For example, a negative exponential distribution, in which there is a negative linear relationship between log(density) and tree size, is generally indicative of fairly constant rates of growth, recruitment and mortality (Rubin et al., 2006). By contrast, episodic recruitment (on a decadal scale) produces multi-modal distributions.

One particularly promising species for the studies of population structure is *Callitris columellaris* F. Muell. (*sensu* Farjon, 2005), the native cypress pine that occurs in diverse climates, landscape

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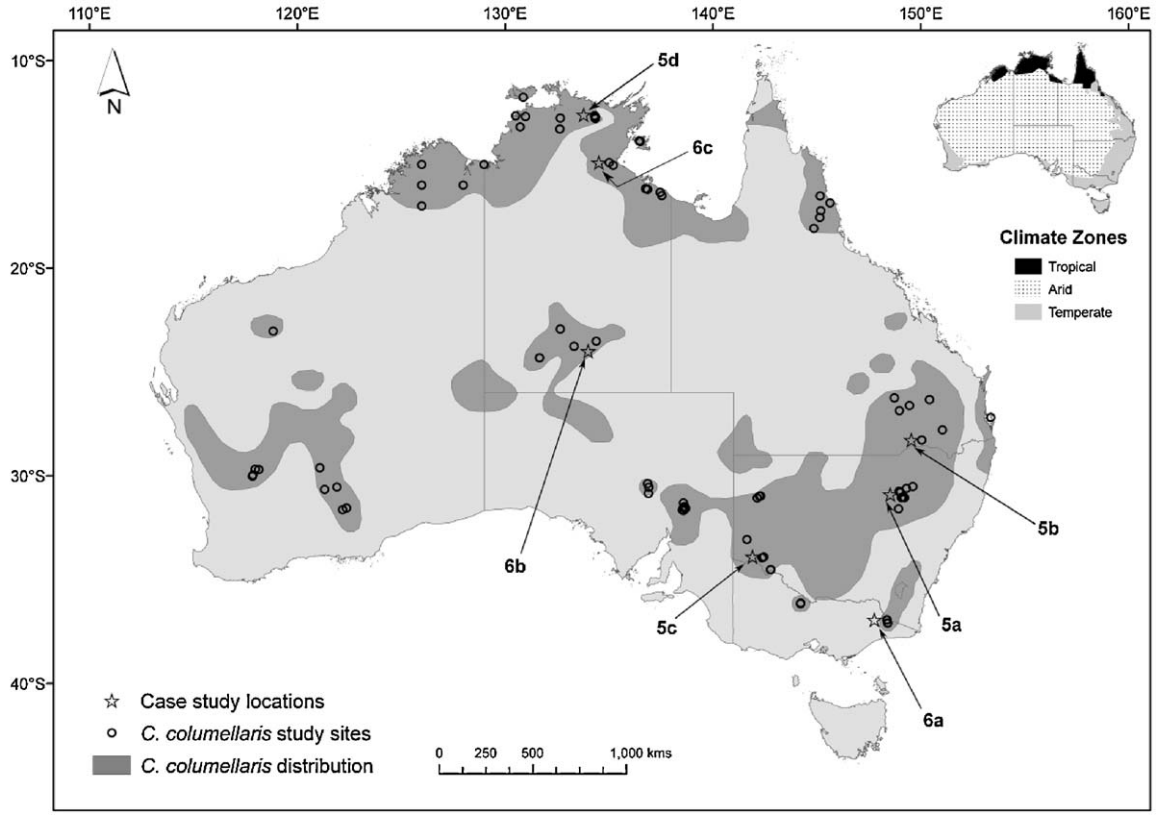

Fig. 1. Distribution of *Callitris columellaris* and location of sample sites (circles). Latitude and longitude are indicated on left and top axes respectively. The stars represent our case study sites, labelled according to the figure in which they are presented. Where sampling sites are very close together, symbols are superimposed. The small map at top right shows the major Köppen–Geiger climate zones (Kottek et al., 2006).

settings and soil types and under widely varying management histories (Bowman and Harris, 1995; Thompson and Eldridge, 2005). *Callitris* is a genus of the Cupressaceae family, and is found only in Australia and New Caledonia. It is estimated that *Callitris* forest and woodland occupied 40,000 km^2 of Australia at the time of European settlement, of which 20% has since been cleared (Department of the Environment and Water Resources, 2007). The most widespread species is *C. columellaris* (*sensu* Farjon, 2005), although some regard this as a clade of three species, *Callitris intratropica*, *Callitris glaucophylla* and *C. columellaris sensu stricto* (Pye et al., 2003; Piggin and Bruhl, 2010). *C. columellaris* has a wide geographic range across continental Australia, reflecting its extreme drought tolerance (Clayton-Greene, 1983; Brodribb et al., 2010), yet its distribution is fragmentary as a result of its sensitivity to disturbance (Bowman and Harris, 1995). Key aspects of the biology of *C. columellaris* that make it a sensitive bio-indicator of environmental change since European settlement of Australia are (a) its lifespan of 200+ years (Lacey, 1973; Bowman and Panton, 1993; Lunt et al., 2006; Cullen and Grierson, 2009); (b) marked annual variation in seed production and seed viability (Hawkins, 1966; Lacey, 1973); (c) non-serotinous cones (Lacey, 1973); (d) very limited seed dispersal (Stocker, 1966; Bowman et al., 1988); (e) absence of a soil seedbank (Hawkins, 1966; Stocker, 1966; Lacey, 1973); and (f) seedlings are readily killed by fire, and vulnerable to introduced herbivores, particularly sheep, goats and rabbits (Lacey, 1973; Bowman et al., 1988; Bowman and Panton, 1993; Russell-Smith, 2006). Fire can also reduce seed production of surviving trees for 5 years or more (Hawkins, 1966). In the absence of fire, *C. columellaris* can reproduce rapidly, and it is classed as an invasive native species in some agricultural areas (Harris and Lamb, 2004; McHenry et al., 2006). By contrast, frequent fires have resulted in a decline in abundance or extirpation in some areas (Bowman et al., 2001; Graham, 2001; Russell-Smith, 2006; Prior et al., 2007, 2010). *C. columellaris* is also in decline in much of the drier part of the continent, where seedling establishment is precarious, occurring only during unusually wet periods, and where browsing by introduced sheep, goats and rabbits has imposed additional seedling mortality on what are often small, isolated populations (Zimmer, 1944; Read, 1995; Allcock and Hik, 2004; Briggs et al., 2008). In the temperate zone, stands have been cleared for agriculture and some areas set aside for timber production.

In this study, we synthesise existing knowledge and create a continental framework based on the standardised collection of stand structure and associated environmental data from 90 *C. columellaris* populations across Australia (Fig. 1). We determine the relative importance of climate, soil fertility and competition to *C. columellaris* basal area and juvenile density (seedlings and saplings) across the continent and describe variation in soils and disturbance regimes among tropical, arid and temperate climate zones (Kottek et al., 2006). For each of the three climate zones we also examine differences in *C. columellaris* stand structures and infer differences in recruitment and mortality. Demographic data were collected from additional populations to serve as case studies to illustrate demographic responses to specific key disturbances such as fire and grazing. Collectively, these data enable us to consider how European management has changed woodland ecosystems across the Australian continent.

2. Materials and methods

2.1. Study sites and transects

We targeted regions across Australia known to contain populations of *C. columellaris* F. Muell. (*sensu* Farjon, 2005) and that