

Dynamics of Murray-Darling floodplain forests under multiple stressors: The past, present, and future of an Australian icon

Ralph Mac Nally,¹ Shaun C. Cunningham,¹ Patrick J. Baker,¹ Gillis J. Horner,¹ and James R. Thomson¹

Received 7 January 2011; revised 16 March 2011; accepted 4 April 2011; published 14 June 2011.

[1] We review the human actions, proximal stressors and ecological responses for floodplain forests Australia's largest river system—the Murray-Darling Basin. A conceptual model for the floodplain forests was built from extensive published information and some unpublished results for the system, which should provide a basis for understanding, studying and managing the ecology of floodplains that face similar environmental stresses. Since European settlement, lowlands areas of the basin have been extensively cleared for agriculture and remnant forests heavily harvested for timber. The most significant human intervention is modification of river flows, and the reduction in frequency, duration and timing of flooding, which are compounded by climate change (higher temperatures and reduced rainfall) and deteriorating groundwater conditions (depth and salinity). This has created unfavorable conditions for all life-history stages of the dominant floodplain tree (*Eucalyptus camaldulensis* Dehnh.). Lack of extensive flooding has led to widespread dieback across the Murray River floodplain (currently 79% by area). Management for timber resources has altered the structure of these forests from one dominated by large, widely spreading trees to mixed-aged stands of smaller pole trees. Reductions in numbers of birds and other vertebrates followed the decline in habitat quality (hollow-bearing trees, fallen timber). Restoration of these forests is dependent on substantial increases in the frequency and extent of flooding, improvements in groundwater conditions, re-establishing a diversity of forest structures, removal of grazing and consideration of these interacting stressors.

Citation: Mac Nally, R., S. C. Cunningham, P. J. Baker, G. J. Horner, and J. R. Thomson (2011), Dynamics of Murray-Darling floodplain forests under multiple stressors: The past, present, and future of an Australian icon, *Water Resour. Res.*, 47, W00G05, doi:10.1029/2011WR010383.

1. Introduction

[2] Floodplain forests occupy the interface zone between uplands and rivers, providing important sites for the exchange of nutrients and material between these distinct ecosystems [Ballinger and Lake, 2006]. The inundation of floodplains ranges from regular (e.g., tropical wet seasons) to highly irregular (e.g., arid zones), providing strong selection on the kinds of plants, animals, and microorganisms that can persist [Parolin *et al.*, 2004; Ballinger and Mac Nally, 2006]. In arid regions, such as southeastern Australia, southwestern North America, northeastern Africa, and South Asia, floodplain forests play a key role in supporting regional biodiversity and productivity. Such forests often have higher productivity than surrounding vegetation due to the additional water from floods and shallow groundwater [Tockner and Stanford, 2002], which supports a distinct flora and fauna that increases regional biodiversity [Sabo *et al.*, 2005].

[3] The dynamics of river systems and their associated floodplains affect the quantity and quality of forest and water resources, the biota dependent on these ecosystems, and the terrestrial and aquatic ecosystems in adjacent parts of the landscape [McGinness *et al.*, 2010]. Over the past century, there have been increasing human demands on floodplains to supply water through pumping, diversions, and dams. Changes in flow regimes and volumes have led to the widespread dieback of many floodplain forests, particularly in arid regions [Cunningham *et al.*, 2009b; Holland *et al.*, 2009; González *et al.*, 2010]. Dieback, or substantial change in vegetation structure and composition, can be exacerbated by interactions with other stressors, such as climate change and changing land use [Merritt and Cooper, 2000; Merritt and Poff, 2010; Stromberg *et al.*, 2010].

[4] Floodplain forests are often selected preferentially for agricultural development because they are “accumulators” of moisture and nutrients, so that their proportional representation in regions may be relatively reduced [Mackay and Eastburn, 1990]. Increases in human demands for water and, in many areas, predicted decreases in future precipitation coupled with higher temperatures, suggest further ecosystem degradation and biodiversity decline in coming decades [Palmer *et al.*, 2008]. The

¹Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Clayton, Victoria, Australia.

combination of characteristics of floodplains (usually low elevations, relatively moist, fertile soils) that are attractive to humans renders them subject to multiple, concurrent stressors.

[5] The Murray-Darling Basin is Australia's largest river system, stretching from south-central Queensland to South Australia (25°S–37°S, 139°E–152°E); the basin covers about 10⁶ km² (14% of the Australian continent). The landscape of the basin is composed of a mosaic of riparian, floodplain, and upland ecosystems, much of which has been severely modified by human actions over the last century [McAlpine et al., 2009].

[6] The floodplain forests of the Murray-Darling Basin have been negatively affected by a range of anthropogenic stressors, including river regulation and water extraction, broadscale land management actions across the whole basin, and recent changes in climate and weather patterns [Cai and Cowan, 2008a; Vaughan et al., 2009; Ackerly et al., 2010; Camilleri et al., 2010]. None of these stressors is unique to the basin; all have been documented in other major floodplain ecosystems around the world [Foley et al., 2005; Palmer et al., 2008]. However, there are only a few places (e.g., the southwestern United States) where all of these stressors have occurred synchronously and so intensely over such a relatively short period of time. As such, an assessment of the past, present, and the potential future of the Murray-Darling Basin is useful in anticipating the impacts such stressors, and their interactions, in other major floodplain systems of the world.

[7] In this paper, we synthesize results on the population viability and stand condition of river red gum (*Eucalyptus camaldulensis* Dehnh.), the dominant tree species of the floodplains of the Murray-Darling Basin. We present a conceptual model within which our understanding of the system is summarized, and we relate how natural resource management and the state of river red gum forests are inextricably linked to biodiversity in these ecosystems. Our main focus is on the remnant river red gum forests of the Victorian Murray River (Figure 1), which are the primary management concern in *The Living Murray* program of the Murray-Darling Basin Commission [Murray-Darling Basin Commission, 2005]. There are extensive river red gum floodplains in adjacent states (New South Wales, South Australia), to which we refer where necessary, but the knowledge is more complete and consistent for the Victorian Murray River floodplain forests.

2. A Conceptual Model

[8] Over the past decade, there has been a wide range of studies to describe and understand the complex ecological processes operating on the Murray River floodplains. The work has been multidisciplinary, from ecology, population biology, hydrology, climatology, and environmental engineering to remote sensing and forestry. To organize the varied aspects of this research, we developed a conceptual model that identifies the key components, processes, and drivers of the floodplain forests of the Murray-Darling Basin (Figure 2). The model is based on three levels: (1) human actions that are either direct, such as river regulation and forest management, or indirect, such as anthropogenic climate change (Figure 2, octagons); (2) ecological stressors

arising from those human actions (Figure 2, rectangles); and (3) consequent ecological responses. The latter are focused on the population viability of river red gum (Figure 2, shaded oval), stand structure, and stand condition. We begin by briefly considering the impacts of human actions and describe how these have affected the ecological stressors. We conclude by outlining effects on the river red gum forests and floodplain biodiversity.

3. Anthropogenic Actions

3.1. Climate Change

[9] To determine how climate has changed across the Murray River floodplain, we selected four extensive floodplains, which cover the range of climates along the river: Lindsay Island–Wallpolla Island (centered on 34°12'S, 141°30'E), Hattah Lakes (34°42'S, 142°24'E), Gunbower Island (35°45'S, 144°18'E), and Barmah-Millewa Forest (35°51'S, 145°03'E, Figure 1). Data on rainfall, temperature, and modeled potential evapotranspiration (ET) [Allen et al., 1998] were obtained from SILO (Queensland State Government, Department of Natural Resources and Mines, accessed April 2010) for the period 1889–2009. We used daily maximum temperature because these reflect the greatest physiological stress for the river red gum and were highly correlated ($r > 0.83$) with the daily minimum temperatures.

[10] We present information on annual anomalies. To represent climatic anomalies, the Australian Bureau of Meteorology typically uses averages from the period 1961–1990 (e.g., <http://www.bom.gov.au/cgi-bin/climate/change/time-series.cgi>, accessed May 2010). However, the choice of a baseline is arbitrary and, in examining the time series, we noted that the 54 year period 1943–1996 was comparatively stable in both maximum temperature and rainfall, so we have used this longer period for our analyses.

[11] The patterns of temporal variability in temperature are similar among the four floodplains (Figure 3), so that the average conditions provide a reasonable representation of the broader regional trajectory. There has been a prolonged decline in rainfall since 1997 (Figure 3a), which is consistent with trends across southeastern Australia [Cai and Cowan, 2008a].

[12] The two decades prior to 1910 saw temperatures between 1.0°C and 1.5°C above the baseline, while values between 1910 and 1942 averaged about 0.5°C above the baseline (Figure 3a). During the baseline period (1943–1996), temperatures fluctuated above and below the mean for periods of differing length (Figure 3b). Temperatures rose rapidly (currently 1.5°C above baseline) and possibly at an accelerating rate since 1997 (Figure 3b).

[13] Potential ET is an estimate of the atmospheric demand for water that a plant has to meet or to avoid, and, therefore, reflects the stresses that the forests, woodlands, and wetlands of the floodplain experience better than rainfall or temperature alone. The conjunction of decreasing rainfall and increasing temperatures led to a near monotonic increase in ET deficit since the mid-1990s (Figure 3c).

3.2. River Regulation and Water Extraction

[14] Like most floodplains, the regulation of the Murray River in southeastern Australia has reduced peak flows, and

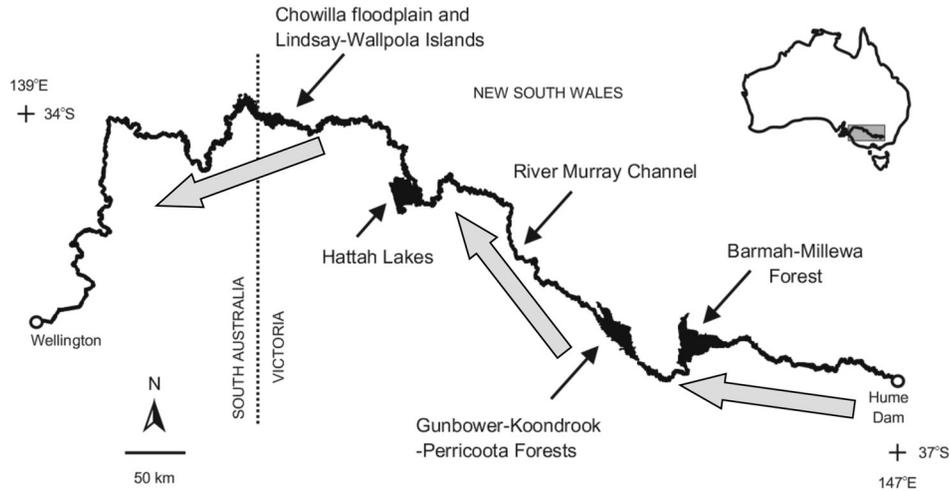


Figure 1. Locations of extensive river red gum floodplain forests along the Murray River of southeastern Australia. The Murray River flows from the Hume Dam to the ocean at Wellington, and forms the border between Victoria and New South Wales (flow direction indicated by gray arrows).

the historical frequency (35%–62%) and duration (40%–80%) of extensive floods that connect the Murray River to its anabranches [Maheshwari et al., 1995]. Annual inflows into the Murray River (exclusive of inputs from the Darling River and from the Snowy Mountains scheme) historically, were extremely variable (Figure 4a). That variation has

declined markedly since the late-1990s, mainly due to much-reduced inflows [Cai and Cowan, 2008a]. Diversions (for irrigation, stock, and domestic) grew steadily from the 1920s, especially following the commissioning of the Hume Dam in the upper reaches of the Murray River in the early 1930s [Kingsford, 2000]. By the early 1990s, the state

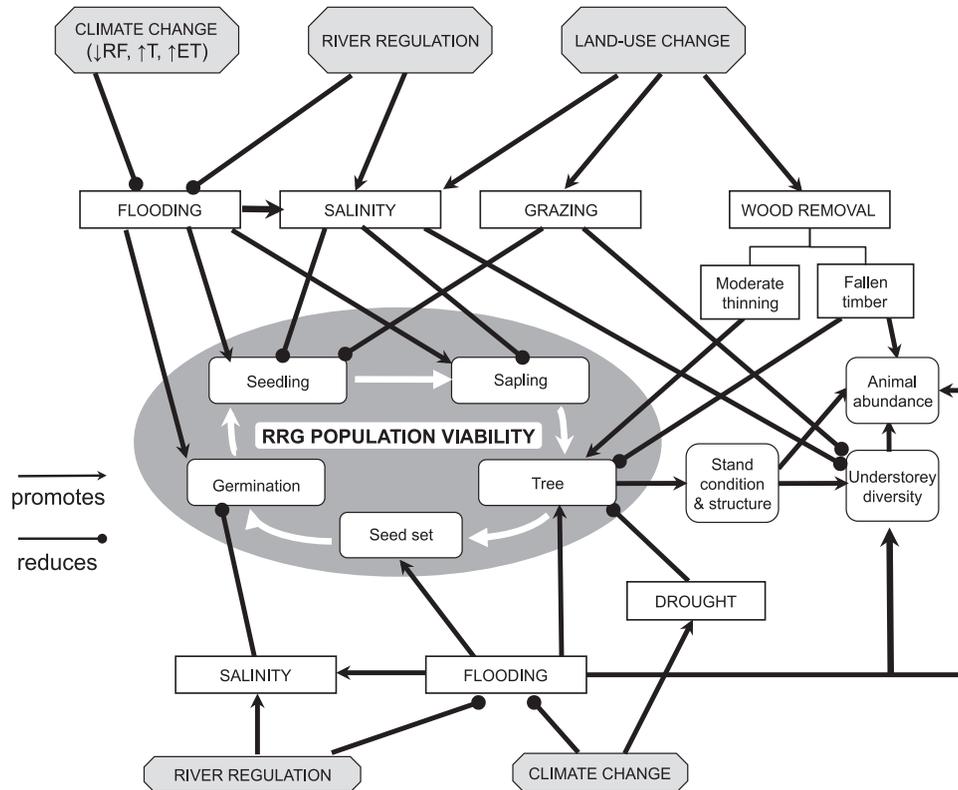


Figure 2. Conceptual model linking human actions (octagons) to ecological stressors (white rectangles) to consequences on river red gum (RRG) population viability and stand condition. Arrows indicate relationships that promote the quantity or process to which the arrow is directed; solid circles have reducing or inhibiting effects. RF is rainfall, ET is evapotranspiration, and T is temperature, with up (increases) and down (decreases) arrows indicating directions of change.

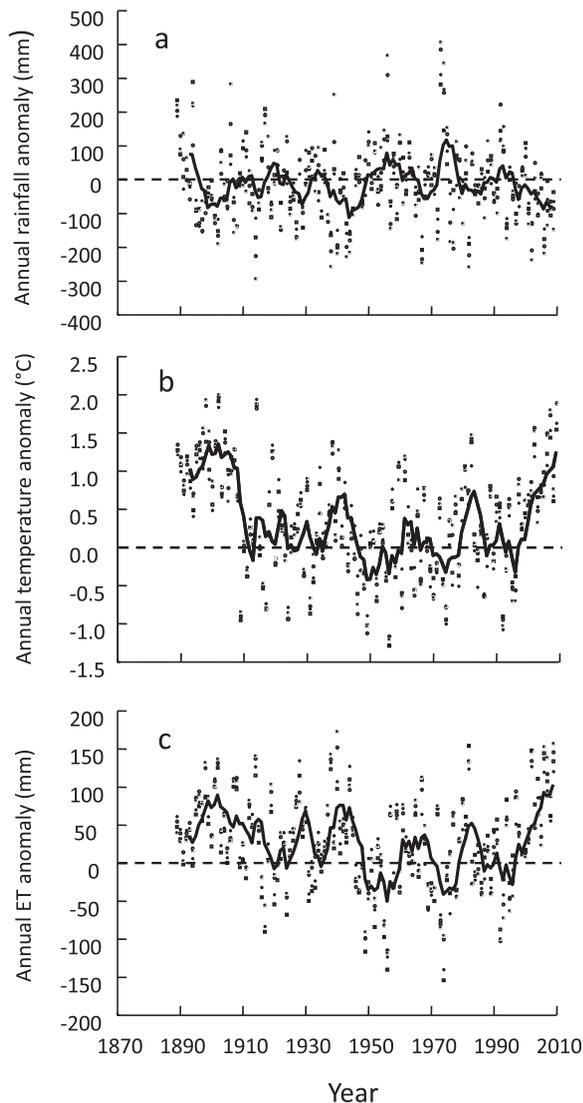


Figure 3. Details of climate dynamics for four Murray River floodplains on the basis of anomalies relative to the average annual values for the 1943–1996 period inclusive. Plots are (a) annual rainfall anomaly, (b) annual temperature anomaly, and (c) annual evapotranspiration (ET) anomaly. Solid lines are 5-year moving averages for the four floodplains. The four floodplains, with symbols indicated, are from west to east: Lindsay-Wallpolla Islands (solid circle, 34°12'S, 141°30'E), Hattah Lakes (open square, 34°42'S, 142°24'E), Gunbower Island (open circle, 35°45'S, 144°18'E), and Barmah-Millewa Forest (solid square, 35°51'S, 145°03'E).

and federal governments imposed a cap on further increases in extractions. However, temperature rises and reduced rainfall since the late 1990s, especially in autumn [Cai and Cowan, 2008b], led to a marked decline in water availability [Cai and Cowan, 2008a] (Figure 4b). For much of the 2000s, extractions exceeded inflows (Figure 4b).

[15] A consequence of these reduced inflows and increased diversions has been the stark reduction in floods. River regulation has had a profound influence on the return times of bankfull discharges. For example, comparing regu-

lated flows with modeled natural flows for a major tributary of the Murray River in New South Wales, the Murrumbidgee River showed a reduction of 43%–56% in the frequency of such flows between 1970 and 1998 (Table 1). The *average* duration between flooding episodes increased twofold since significant water diversions began in major wetland sites across the basin [CSIRO, 2008]. Climate change was not expected to greatly increase the average inter-flood interval in most locations above this development-driven doubling. However, for the Chowilla floodplain in South Australia, the average interval between flooding increased from 2 year (historical interval) to 9 year (regulated) and is projected to increase to 19 year by 2030 [CSIRO, 2008]. The *maximum* period between floods has doubled on average across the basin, but in some important floodplains, such as Barmah-Millewa and the Gunbower-Koondrook-Perricoota Forests, the period has increased from 5 year (historical period) to 11 year (regulated) and is projected to be 21 year by 2030 [CSIRO, 2008]. Since 1990, groundwater depths have declined on important floodplains of the Murray River, often below the effective reach of the roots of the trees, and an attendant rise in salinity, with salinity often exceeding that of seawater (30 mS cm^{-1}) in the lower Murray River (Table 2).

3.3. Land-Use Change and Forest Management

[16] The Murray-Darling Basin has lost at least 1.2×10^{11} trees since European settlement in the late 1700s [Walker *et al.*, 1993]. The loss of forests and woodlands has been selective, with lowland woodlands in humid areas on better soils being almost entirely converted to agriculture [Environment Conservation Council, 2001]. Two major consequences of this regional-scale land conversion have been substantial declines in biodiversity [Bennett *et al.*, 1998; Barrett *et al.*, 2003; Mac Nally *et al.*, 2009] and the secondary salinization of large swathes of plains systems [Bennett *et al.*, 2006]. For example, of the 1.3×10^7 hectare (ha) of Victoria within the Murray-Darling Basin, 202,000 ha was salinized in 1999 and 840,000 ha is projected to be affected by 2050 [Murray-Darling Basin Ministerial Council, 1999].

[17] The floodplain forest systems have been spared the severest of total tree clearance. For example, 90,000 ha (60% of historical extent) of the floodplain forest in northern Victoria [Victorian Environmental Assessment Council (VEAC), 2008] and 236,000 ha (68% of historical extent) of the floodplain forest in the Riverina of southern New South Wales remains [Natural Resources Commission (NRC), 2009b]. This relatively high areal retention is due to the management of river red gum forests for timber extraction (poles, posts, house frames, railway sleepers, and firewood), which has been a major activity for almost 200 years [Crabb, 1997]. The growth rates of river red gums in the Barmah Forest and on Gunbower Island have decreased by up to 40% over the long dry period after 1996 (Table 3). For the major production areas in Victoria, the licensed sawlog extractions exceeded estimated productivity by 43% [VEAC, 2008], leading to recommendations for the complete closure of the Barmah Forest and for a 15% reduction in harvestable area at Gunbower Island (Table 3).

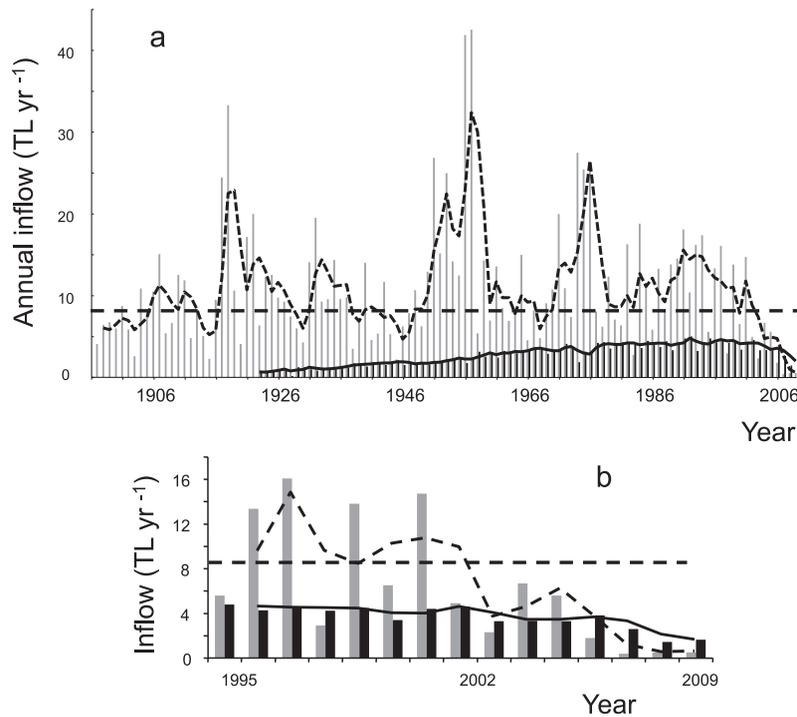


Figure 4. Time series of total annual inflows in teralitres (TL yr^{-1} , dashed line and gray bars), excluding inflows from the Darling River and from Snowy River diversions, into and total diversions out of (solid line and black bars) the Murray River (a) over the last century and (b) detail of the patterns since the onset of the long dry period in the mid-1990s. Three-year moving averages are provided for each data set. Dashed lines are the average total inflow prior to 1997.

4. Proximal Ecological Stressors

4.1. Flooding

[18] Floods are critical to the life cycle of much of the flora and fauna on the floodplains of the Murray-Darling Basin. Although river red gums can germinate after heavy rainfall events, the survival of saplings is much increased by the moist conditions provided by floods in the first few years, which allow the taproot to reach underground water sources and avoid future water stress [Dexter, 1978]. Very little of the river red gum floodplain now experiences extensive (1000s of ha), long-term (>3 mo) flooding. Management agencies have resorted to providing artificial floods to sustain adult trees and to promote the recruitment of saplings. These management floods are of limited areal

Table 1. Numbers of Occasions Between 1970 and 1998 in Which Bankfull Flows Occurred With Regulated Flows and Modeled Natural Flows at Six Gauging Stations Along the Murrumbidgee River in New South Wales, Australia [Page *et al.*, 2005]^a

Station	Natural	Regulated	Percent Reduction
Gundagai	41	19	54
Wagga Wagga	59	26	56
Narrandera	47	22	53
Darlington Point	51	28	45
Hay	35	20	43
Balranald	25	11	56

^aStations are ordered from the most upstream (Gundagai) to the most downstream (Balranald).

extent (100s of ha) and duration (<3 mo) owing to the limited water available for this purpose [Bond *et al.*, 2008].

4.2. Salinity

[19] The Murray-Darling Basin is predominantly semi-arid with variable rainfall and high evaporation, which leads to saline groundwater [Gee and Hillel, 1988]. Impoundments maintain elevated river levels and elevate groundwater levels upstream of them [Jolly, 1996]. Groundwater extraction, which is common in arid and semiarid regions, increases groundwater depth [Gore, 1994]. Reductions in flooding have resulted in a higher dependence of trees on groundwater, which has lowered further the groundwater; this has caused the salinization of soils in areas underlain by saline groundwater (Table 2) [Jolly, 1996]. Riverine systems have received vast amounts of salt from upland areas and the plains, which are deposited in high-order rivers such as the Murray River. River regulation has prevented “flushing flows,” which leach salts from floodplain soils [Overton *et al.*, 2006]. This is particularly important in areas of drying climates, where reduced rainfall is insufficient to leach salts from root zones.

4.3. Grazing

[20] We use the term “grazing” as both grazing of grasses and herbs and browsing on woody seedlings. Grazers can be grouped into: (1) domestic livestock grazing on floodplains; (2) invasive species (primarily the European rabbit *Oryctolagus cuniculus* L., but also the European

Table 2. Characteristics of Groundwater Bores From Four Floodplains Along the Murray River Floodplains^a

Region	N	Groundwater in 1990		Groundwater in 2006	
		Depth (m)	Salinity (mS cm ⁻²)	Depth (m)	Salinity (mS cm ⁻²)
Chowilla and Lindsay/Wallpolla	89	4.3 ± 0.2	26.3 ± 2.5	4.9 ± 0.2	32.0 ± 2.7
Hattah Lakes	60	4.6 ± 0.3	24.0 ± 2.7	5.8 ± 0.3	24.6 ± 2.8
Gunbower Island	34	4.7 ± 0.5	16.3 ± 2.2	6.6 ± 0.5	18.7 ± 2.4
Barmah-Millewa Forest	105	9.0 ± 0.4	2.5 ± 0.5	11.0 ± 0.5	2.8 ± 0.5

^aValues are means ± SE [Cunningham *et al.*, 2011].

brown hare *Lepus capensis* L.); and (3) native mammals (mostly kangaroos, *Macropus fuliginosus* (Desmarest) and *M. rufus* (Desmarest)). Grazing by cattle and sheep on Murray-Darling Basin floodplains began in the 1830s [VEAC, 2008]. Feral rabbits became abundant in the 1890s [Bacon *et al.*, 1994]. Grazing licenses for livestock continue on some of the floodplains [NRC, 2009a]. The grazing of floodplain forests by livestock, sheep, and cattle has demonstrably adverse effects on understorey vegetation, including the saplings of river red gum [Robertson and Rowling, 2000]. The slope of the relationship between an index of floodplain condition (predominantly vegetation indicators) and a standardized measure of grazing intensity was strongly negative (slopes were -0.14 ± 0.02 SE and -0.23 ± 0.02 SE for two geomorphic regions of the river valley) at sites on the Murrumbidgee River floodplains, a major tributary of the Murray River [Jansen and Robertson, 2001]. Rabbit numbers have recovered from the impacts of rabbit hemorrhagic disease virus [Lawrence, 2009], while some native herbivores, such as kangaroos, have been largely restricted to remnant native vegetation, including the floodplain forests [Morgan and Pegler, 2010].

4.4. Wood Removal: Shaping the Forest

[21] Timber management has left river red gum floodplain forests in a much-altered condition. Timber harvesting has resulted in predominantly even-aged stands of straight “poles” with few large trees areas, especially in the more easterly remnant floodplains (Barmah-Millewa Forest and Gunbower Island). Forest structure prior to European settlement is thought to have consisted of relatively few large (diameter at breast height ≥ 1 m), widely spreading trees interspersed with a mosaic of mixed-aged stands of varying sizes [Jacobs, 1955].

[22] River red gum forests have been extensively exploited for firewood for more than a century. In the public forests of the Murray-Darling Basin, approximately 1.15×10^5 t yr⁻¹ of firewood and approximately 1.22×10^5 t yr⁻¹ of timber (including wood chips) are removed [Crabb, 1997]. A conse-

quence of this intense harvesting pressure has been a near-complete elimination of fallen timber (logs and branches ≥ 10 cm diameter and ≥ 1 m long, [Harmon *et al.*, 1986; Mac Nally *et al.*, 2002a]). Measurements and estimates of total current fallen timber loads (2001) ranged between 12 and 24 t ha⁻¹, with a total load of about 4.75×10^6 t in the floodplain forests of the southern Murray-Darling Basin (Table 4). If fallen timber loads prior to European settlement in the nineteenth century were similar to loads found in inaccessible areas of the floodplains of southern New South Wales (~ 125 t ha⁻¹) [Robinson, 1997], then current loads are only 15% of former loads (Table 4). Thorough investigations of nineteenth century literature and diaries provided no more definitive measures of presettlement loads than these estimates [Mac Nally and Parkinson, 2005].

5. Ecological Consequences: River Red Gum Stand Condition and Demography

5.1. Trajectories of Stand Condition

[23] River regulation of the Murray-Darling Basin, which has much reduced flooding frequencies and led to a decline in groundwater availability, has led to the extensive dieback of floodplain forests. The dieback of river red gum forests along the Victorian Murray River floodplain increased from 45% to 70% of the floodplain forests between 1990 and 2009 (Figure 5) [Cunningham *et al.*, 2009a; Cunningham *et al.*, 2011]. In 2009, 79% of the forested area on the Murray River floodplains contained some degree of forest dieback. The proportions of affected areas did not differ substantially between the 1990 and 2003 estimates, but both values were substantially less than the 2006 and 2009 estimates, which were not different (Figure 5). This substantial decline in stand condition since 2003 suggests that the area of dieback will continue to increase unless the frequency and extent of flooding is substantially elevated.

[24] Groundwater depth and salinity are strong predictors of stand condition in river red gum forests [Cunningham *et al.*, 2011]. In the upper, eastern-most Murray region,

Table 3. Timber Harvesting Estimates for River Red Gum^a

Floodplain Forest	Growth Rates (m ³ ha ⁻¹ yr ⁻¹)		Available Areas (ha)		Growth Over Available Areas (m ³ yr ⁻¹)		Sawlogs (m ³ yr ⁻¹)	
	FF	DC	FF	RC	FF	DC	FF	RC
Barmah	0.24	0.14	18,100	0	4,344	2,534	2,970	0
Gunbower Island	0.20	0.12	11,458	9,884	2,292	1,375	1,573	814

^aTimber harvesting estimates are based on the long-term, frequent-flooding (FF) growth rates and on revised estimates under current dry conditions (DC) and recommended changes (RC) adapted from VEAC [2008].

Table 4. Estimates of Fallen-Timber Loads on Southern Murray-Darling Floodplains [Mac Nally et al., 2002a]

Floodplain	Area (ha)	Mean Fallen-Timber Load (t ha ⁻¹)	Floodplain Totals (t)
Barmah Forest	30,000	24.4	741,900
Gunbower Island	21,000	16.0	335,900
Goulburn River	7,000	11.8	83,800
Millewa Forest	33,600	16.8	562,600
Ovens River	10,000	18.7	188,000
Murray Channel	119,480	18.9	2,262,900
Total	221,080	18.9	4,175,100
Unharvested estimates [Robinson, 1997]	442,160	125	27,635,000
Percent remaining		—	15%

where the groundwater is predominantly fresh (<15 mS cm⁻², Table 2), stand condition decreased with increasing groundwater depth. However, the condition of stands in the lower, western-most Murray floodplains improved with increased groundwater depth because of the high salinity of the groundwater (>30 mS cm⁻², Table 2) [Cunningham et al., 2011]. Therefore, effective groundwater management differs across the Murray River floodplain.

[25] In natural germination events, large numbers of seedlings emerge, often in dense copses. The thinning of established trees in river red gum forests has been suggested to improve stand condition and associated ecologically important characteristics. In a 42 year thinning experiment at Barmah Forest, in the more mesic, easterly part of the Murray River floodplains (Figure 1), the thinning of high-density (> 1000 trees ha⁻¹) stands appeared to improve survivorship

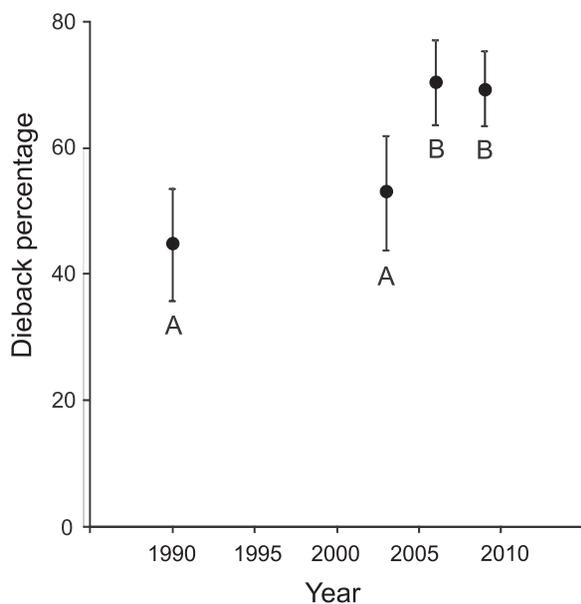


Figure 5. Times series of dieback in river red gum forests across the Victorian Murray River Floodplain. Forest dieback includes all stands where the average tree has less than 80% of its potential crown. Data are adapted from Cunningham et al. [2009a, 2009b]. Bars are standard deviations of estimates. Years with the same letter did not have substantial differences in the extent of dieback using odds ratios >10 (see Table 5).

in the continuing dry conditions [Horner et al., 2010]. Above-ground carbon storage rates were substantially higher (3.1–4.1 t C ha⁻¹yr⁻¹) in all treatments in which the initial density (4000 ha⁻¹) was thinned to less than 1000 trees ha⁻¹. Unthinned forests stored 1.6 ± 0.3 t C ha⁻¹yr⁻¹ [Horner et al., 2010]. The numbers of hollow-bearing trees, which are critical for breeding and shelter for much of the vertebrate fauna of many temperate Australian forests, including river red gum forests [Bennett et al., 1994; Gibbons et al., 2002], were much more prevalent in thinned stands. No hollows were detected in unthinned stands, but there were 20 ± 15 SE hollow-bearing trees ha⁻¹ for the other thinned treatments [Horner et al., 2010].

[26] These results were mirrored in planting experiments where treatments were of different initial densities at Barmah over the same period [Horner et al., 2009]. Therefore, manipulations of stand density may provide some temporary improvement in condition, but increased water availability through flooding is ultimately required to mitigate, if not reverse, the negative impacts of a rapidly drying climate and water extractions.

5.2. Population Processes of the River Red Gum

[27] Reduced water availability and quality caused by river regulation, salinization, and a drying climate has created unfavorable conditions for all stages of the life history of the river red gum. Recruitment appears to be affected by the interaction of reduced flooding, grazing, and soil salinity. In September 2006, we established two pairs of grazed and ungrazed (3 × 3 m) plots at each of six creeks across the Lindsay-Wallpolla Islands floodplain. Ungrazed plots were fenced with mesh to 1.8 m high to exclude all mammalian herbivores. Half of the creeks were experimentally flooded by the responsible natural resource management agency. Plots were surveyed eight times between October 2006 and June 2008. Sediment salinity can influence population viabilities of floodplain plants by limiting germination and by killing seedlings [Cramer and Hobbs, 2002], so we measured sediment salinity. We used a Weibull survival model with flooding and grazing as factors and with sediment salinity as a covariate. The positive effects of flooding on survival (on a log (survival) scale: 2.04 ± 1.27 SD) were nullified by grazing (-1.28 ± 0.49) and sediment salinity (-0.42 ± 0.21). Given the extensive dieback of mature trees, there is an urgent need to enhance seedling and sapling recruitment. The restoration of population viability needs to consider the effects of these multiple interacting stressors that limit recruitment.

6. Ecological Consequences: Floodplain Biodiversity

[28] The floodplain biota is affected by several aspects of stand structure and condition and by flooding. The structural characteristics of the forests, especially the much-modified “pole” versus “spreading tree” forms, and the removal of fallen timber have demonstrable effects on floodplain vertebrates [Mac Nally and Horrocks, 2007]. Avian assemblage structure is likely to change substantially because different birds species respond differently to stand structure, the availability of shrubs, etc. For example, the encroachment of invasive *Tamarix* spp. into *Populus-Salix* forests in the southwestern United States, associated with

increases in groundwater depth due to pumping, led to declines in species richness and the number of unique species on the floodplain [Brand *et al.*, 2008]. Vertebrates appear to respond to river red gum stand condition, but flooding per se is indirectly important, probably through increasing the availability of prey invertebrates [Mac Nally and Horrocks, 2008].

6.1. Animals

[29] Small mammals and birds in these floodplain forests prefer higher loads of fallen timber than are typically available in managed forests [Mac Nally *et al.*, 2002b; Lada *et al.*, 2007]. Although not yet teased apart experimentally, this response is likely to be related to increased cover, shelter from predation, and higher availability of food, especially of invertebrates [Mac Nally and Horrocks, 2007]. We manipulated woodloads in thirty 1 ha plots, and monitored them prior to and after the manipulations [Mac Nally, 2001]. Bird assemblages were much affected by fallen-timber loads, with clear differences in avian composition at sites with loads exceeding 40 t ha⁻¹ compared with sites with lower timber loads [Mac Nally and Horrocks, 2007]. The densities of a near-threatened bird species, the brown treecreeper (*Climacteris picumnus*), were substantially higher in all treatments with timber loads ≥40 t ha⁻¹ (Figure 6), which was possibly due to a higher availability of invertebrate prey.

[30] Some vertebrate species appear to respond not only to fallen-timber loads but to flooding and the availability of large trees, which have a much higher probability of bearing hollows upon which the species rely [Horner *et al.*, 2010]. The pole-oriented management in the eastern Murray River floodplains has produced stands that are largely bereft of tree hollows, with follow-on effects on hollow-dependent fauna [Horner *et al.*, 2010]. Tree hollows develop from large, essentially horizontal branches [Vesk *et*

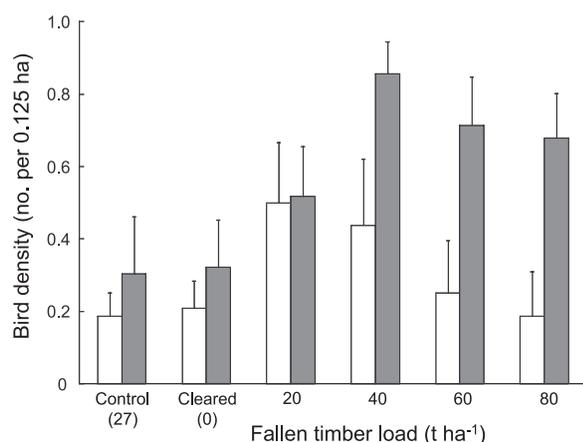


Figure 6. Densities (mean ± SE) of the brown treecreeper (*Climacteris picumnus*) in a mesoscale experiment involving relocation of fallen timber among treatments [Mac Nally, 2006]. There were four replicate 1 ha plots for all treatments except the cleared treatment ($n = 6$), and data are for pre- (open bars) and postmanipulation (hatched bars) surveys. Pre- and postmanipulation means were different for all treatments apart from cleared 20 t ha⁻¹ and the control.

al., 2008], which are deliberately removed by current forest management practices to improve sawlog production [NRC, 2009a].

[31] The most common small-mammal species on river red gum floodplains, the yellow-footed antechinus (*Antechinus flavipes*), a small marsupial carnivore (30–80 g), appears to respond to three factors (Table 5). Antechinuses were more likely to be trapped (a measure of abundance, [Lada *et al.*, 2008a]) at locations with higher fallen-timber loads, around areas of recent flooding, and where there are more large, hollow-bearing trees (Table 5). Females did not produce young in sites with <20 t ha⁻¹, and the most breeding was at sites with the highest fallen-timber loads (80 t ha⁻¹) [Mac Nally and Horrocks, 2008]. The population dynamics of *A. flavipes* appear to be strongly related to the extent and duration of floods [Mac Nally and Horrocks, 2008]. Population surges in *A. flavipes* probably occur because of elevated availabilities of food. Flooding appears to cause irruptions of both abundances, and biomass of beetles that contribute to higher food availability for the ground-feeding, insectivorous antechinuses [Ballinger *et al.*, 2005, 2010]. These increases in beetles are greater in areas that are inundated for longer periods. For example, the number of beetles was six times higher in extensively flooded sites compared with unflooded sites, while biomasses were almost 100-fold higher (Table 6). Females of *A. flavipes* have as many as 15 young in a season (mean = 10.4 ± 2.2 SD), which is consistent with a life history of opportunistic, explosive breeding, so populations are capable of responding rapidly to fluctuations in resource availability. Therefore, when floods generate high invertebrate flushes, antechinus survivorship is high and densities increase sharply.

[32] Birds respond directly to river red gum stand condition [sensu Cunningham *et al.*, 2009b]. We looked at four measures of avian response: (1) the total number of species recorded over five visits; (2) the total records of all species over five visits; (3) the number of species showing any breeding activities; and (4) total breeding activity summed over all species. We used quantile regression for the median [Koenker, 2010] because of the non-normality of the

Table 5. Dependence of Trapping Rates (Genders Combined) of the Yellow-Footed Antechinus on Site Characteristics on the Murray River Floodplain^a

Predictor Variable	Coefficient ± SD ^b	Change in Capture Odds (95% CI) ^c
Distance to floods (km)	-0.45 ± 0.19	-36% (-56, -8)
Fallen-timber load (t ha ⁻¹)	0.31 ± 0.07	+36% (19, 56)
Numbers of large trees (≥ 60 cm)	0.17 ± 0.07	+19% (3, 36)

^aResults from a Bayesian binomial response model on the basis of a survey of one hundred eighty-three 0.25 ha plots [Lada *et al.*, 2007].

^bCoefficients are estimated changes in the log-odds transformed capture rate per 1 SD change in the predictor variable.

^cExpected change in the odds of capturing antechinus per unit change in the predictor variable (e.g., the odds of capturing an antechinus in a single trap night increase by 36% for every additional ton per hectare of fallen timber). Values were derived directly from the regression coefficients (odds ratio = exp (coefficient/SD), where SD is the SD of the predictor variable). Ninety-five percent CI = 95% Bayesian credible interval: 95% of the posterior probability mass of the parameter estimates lies within these limits.

Table 6. Abundances and Biomasses of Beetles in Areas of No, Medium, and Extensive Flooding on the Barmah Floodplain in 2001 [Ballinger *et al.*, 2005]^a

Variable, Treatment	N (Sites)	Mean (Range)
Abundance ^b		
No flooding	7	8 (6–11)
Medium flooding	8	14 (11–17)
Extensive flooding	9	47 (38–57)
Biomass ^c		
No flooding	7	35 (19–63)
Medium flooding	8	75 (43–132)
Extensive flooding	9	2981 (1808–4915)

^aFlooding definitions: no flooding: soil dry and compacted, ground cover of dry grasses, no aquatic-insect exuviae evident; moderate flooding: soil dry, ground covering generally of verdant grass but may be some dead aquatic plants present, few aquatic-insect exuviae present, may be some silt deposited by floodwaters evident; extensive flooding: damp soil, considerable growth of aquatic plants, many exuviae of aquatic insects attached to tree trunks, often extensive silt deposition, “watermark” left on tree trunks.

^bAbundance = individuals (0.022 m² trap surface area)⁻¹ (5 d)⁻¹.

^cBiomass = mg (0.022 m² trap surface area)⁻¹ (5 d)⁻¹.

data. After taking into account the influence of other covariates (e.g., numbers of tree hollows, fallen-timber loads), stand condition (scored on a scale of 0–15) had a positive effect for the four response variables. The estimated slopes (25% and 75% credible intervals) were: (1) total number of species recorded, 0.70 (0.15–1.31); (2) total records of all species (i.e., the numbers of individuals of all species seen over all visits), 4.00 (0.38–5.77); (3) number of species showing any breeding activities, 0.33 (0.20–0.63); and (4) total breeding activity summed over all species, 0.60 (0.10–2.46).

[33] The yellow-footed antechinus also responds to stand condition. We used data from extensive surveys of 268 sites in Barmah, Millewa, Gunbower, Koondrook, and Perricoota Forests [Lada *et al.*, 2007, 2008a, 2008b, 2008c]. The captures per trap-night of females were positively associated with stand condition [quantile regression: 0.005, bounds = (0.001–0.014)], and even more strongly for the rare females that reach a second breeding season [quantile regression: 0.007, bounds = (0.006–0.010)]. Males, all of which die after breeding, were negatively associated with stand condition [quantile regression: -0.013, bounds = (-0.022, 0.0002)], which is consistent with their ejection from the home ranges of territorial females and their extensive searching for mates during the short breeding season [Lada *et al.*, 2007].

6.2. Floodplain Understorey Plants

[34] The drying climate is likely to exacerbate forest dieback and lead to landscape-scale changes in the population viability of trees and forest structure. The processes responsible for forest dieback (reduced flooding and soil salinization) may result in a change in understorey plant assemblages. At Wallpolla Island, in the more xeric west of the Murray River floodplains (Figure 1), the richness of native understorey plants was strongly negatively associated with plant area index, a measure of canopy coverage (Table 7). Flooding had a pronounced positive effect on native plant richness, more than doubling the number of species

Table 7. Predictors of Species Richness of Native Understorey Plants at the More Xeric, Westerly Wallpolla Island Determined by Bayesian Model Averaging [Raftery *et al.*, 1997]

Predictor Variable ^a	Pr (Inclusion) ^b	Estimated Coefficient (± SE) ^c
Plant area index	1.00	-0.19 ± 0.05
Live basal area	0.20	-0.01 ± 0.04
Percent live basal area	0.26	-0.02 ± 0.04
Tree density	0.16	-0.01 ± 0.02
Flood	1.00	0.71 ± 0.09

^aPlant area index is the area of leaves and stems per unit ground area; percent live basal area is the proportion of the total basal area of a stand containing live stems; flood is the application of an experimental flood.

^bPosterior probability that the predictor variable is included in the best predictive model. Variables with Pr (inclusion) > 0.75 were identified as key predictors.

^cCoefficients are based on the weighted posterior mean coefficient of retained models produced by Bayesian model averaging.

compared to unflooded sites, while there was a weaker negative effect of increasing canopy cover (Table 7).

[35] Structural heterogeneity among stands is a strong predictor of species diversity at the patch-scale [Connell, 1978; Petraitis *et al.*, 1989]. Manipulating forest structure through silvicultural thinning reduces tree mortality, and enhances wildlife habitat quality and aboveground carbon storage [Horner *et al.*, 2010]. Therefore, combinations of thinning and restoration flooding treatments should create a larger variety of forest structures that will enhance plant species richness and functional diversity.

7. Conclusions

[36] The ecology of the floodplain forests along the Murray River has been drastically changed by a combination of anthropogenic actions (Figure 2). Increasing river regulation and water extraction and a drying climate have reduced the frequency and extent of flooding. Forest management has altered forest structure from one dominated by large, spreading trees, interspersed with a mosaic of mixed-aged patches, to one of even-aged stands of slender “poles” with few large trees and low fallen timber loads. River red gum forests have undergone extensive dieback (70% of the forest) and recruitment events are rare on the floodplains due to reduced flooding frequencies, increasing soil and groundwater salinity and ongoing grazing. These pronounced structural changes to the forest have led to declines in the abundance, richness, and breeding activity of birds and mammals, and have shifted the understorey toward a terrestrial flora dominated by weeds. The lack of current regeneration means that there is a substantial risk of complete forest loss as the older trees senesce and die without replacement. The restoration of these forests is dependent on substantial increases in the frequency and extent of flooding, re-establishing a diversity of forest structures and consideration of the interacting stressors of grazing and salinity.

[37] **Acknowledgments.** This work was supported by a number of grants, including: Australian Research Council (LP0561958, A19927168, and DP0984170), the Murray-Darling Basin Commission (R7007), and the Hermon Slade Foundation (HSF_02_3). We thank Michael Roderick of the Australian National University for extending us an invitation to contribute to this Special Issue. A large number of colleagues assisted many aspects of this work: We are very appreciative of the efforts of Andrea Ballinger, Charlie Coarser, John Elias, Greg Horrocks, Sommer Jenkins,

Sam Lake, Hania Lada, and Rachael Nolan. Ian Lunt provided helpful advice, as did a number of reviewers and the associate editor. This is contribution 223 from the *Australian Centre for Biodiversity* at Monash University.

References

- Ackerly, D. D., S. R. Loarie, W. K. Cornwell, S. B. Weiss, H. Hamilton, R. Branciforte, and N. J. B. Kraft (2010), The geography of climate change: Implications for conservation biogeography, *Diversity and Distribution*, 16, 476–487.
- Allen, R. G., L. S. Pereira, D. Raes, and M. Smith (1998), Crop evapotranspiration: Guidelines for computing crop water requirements, *UN FAO Irrig Drain. Pap.* 56, 290 pp., Rome.
- Bacon, P. E., K. Ward, P. Craven, M. Harper, and M. Bone (1994), Floodplain land-use issues in the Murray-Darling Basin, in *Murray-Darling Basin Floodplain Wetlands Management*, edited by T. Sharley and C. Higgins, pp. 76–87, Murray-Darling Basin Comm., Canberra, ACT, Australia.
- Ballinger, A., and P. S. Lake (2006), Energy and nutrient fluxes from rivers and streams into terrestrial food webs, *Mar. Freshwater Res.*, 57, 15–28.
- Ballinger, A., and R. Mac Nally (2006), The landscape context of flooding in the Murray-Darling Basin, *Adv. Ecol. Res.*, 39, 85–105.
- Ballinger, A., R. Mac Nally, and P. S. Lake (2005), Immediate and longer-term effects of managed flooding on floodplain invertebrate assemblages in south-eastern Australia: Generation and maintenance of a mosaic landscape, *Freshwater Biol.*, 50, 1190–1205.
- Ballinger, A., R. Mac Nally, and P. S. Lake (2010), Decay state and inundation history control assemblage structure of log-dwelling invertebrates in floodplain forests, *River Res. Appl.*, 26, 207–219.
- Barrett, G., A. Silcocks, S. Barry, R. Cunningham, and R. Poulter (2003), *The New Atlas of Australian Birds, Birds Australia*, 824 pp., Royal Australasian Ornithologists Union, Melbourne, Australia.
- Bennett, A. F., L. F. Lumsden, and A. O. Nicholls (1994), Tree hollows as a resource for wildlife in remnant woodlands: Spatial and temporal patterns across the northern plains of Victoria, Australia, *Pac. Conserv. Biol.*, 1, 222–235.
- Bennett, A. F., G. Brown, L. Lumsden, D. Hespe, S. Krasna, and J. Silins (1998), Fragments for the future: Wildlife in the Victorian Riverina (the Northern Plains), Dep. Nat. Resour. Environ., Melbourne, Vic., Australia.
- Bennetts, D. A., J. A. Webb, D. J. M. Stone, and D. M. Hill (2006), Understanding the salinisation process for groundwater in an area of south-eastern Australia, using hydrochemical and isotopic evidence, *J. Hydrol.*, 323, 178–192.
- Bond, N. R., P. S. Lake, and A. H. Arthington (2008), The impacts of drought on freshwater ecosystems: An Australian perspective, *Hydrobiologia*, 600, 3–16.
- Brand, L. A., G. C. White, and B. R. Noon (2008), Factors influencing species richness and community composition of breeding birds in a desert riparian corridor, *Condor*, 110, 199–210.
- Cai, W., and T. Cowan (2008a), Evidence of impacts from rising temperature on inflows to the Murray-Darling Basin, *Geophys. Res. Lett.*, 35, L07701, doi:10.1029/2008GL033390.
- Cai, W., and T. Cowan (2008b), Dynamics of late autumn rainfall reduction over southeastern Australia, *Geophys. Res. Lett.*, 35, L09708, doi:10.1029/2008GL033727.
- Camilleri, S., J. Thomson, and R. Mac Nally (2010), The interaction between land use and catchment physiognomy: Understanding avifaunal patterns of the Murray-Darling Basin, Australia, *J. Biogeography*, 37, 293–304.
- Connell, J. H. (1978), Diversity in tropical rain forests and coral reefs, *Science*, 199, 1302–1310.
- Crabb, P. (1997), Murray-Darling Basin Resources, Murray-Darling Basin Comm., Canberra, ACT, Australia.
- Cramer, V. A., and R. J. Hobbs (2002), Ecological consequences of altered hydrological regimes in fragmented ecosystems in southern Australia: Impacts and possible management responses, *Austral Ecol.*, 27, 546–564.
- CSIRO (2008), Water availability in the Murray-Darling Basin: A report to the Australian Government, 67 pp., Commonw. Sci. Ind. Res. Organ. Publ., Canberra, ACT, Australia.
- Cunningham, S. C., R. Mac Nally, P. Griffioen, and M. White (2009a), Mapping the condition of river red gum (*Eucalyptus camaldulensis* Dehnh.) and black box (*Eucalyptus largiflorens* F. Muell.) stands along the Murray River floodplain: Stand condition in 2009 and backcasting to 2003 and 2008, 60 pp., Aust. Centre Biodiversity, Monash Univ., Melbourne, Vic., Australia.
- Cunningham, S. C., R. Mac Nally, J. Read, P. J. Baker, M. White, J. R. Thomson, and P. Griffioen (2009b), A robust technique for mapping vegetation across a major river system, *Ecosystems*, 12, 207–219.
- Cunningham, S. C., J. R. Thomson, R. Mac Nally, J. Read, and P. J. Baker (2011), Groundwater change forecasts widespread forest dieback across an extensive floodplain system, *Freshwater Biol.*, 56, doi:10.1111/j.1365-2427.2011.02585.x.
- Dexter, B. D. (1978), Silviculture of the river red gum forests of the central Murray floodplain, *Proc. R. Soc. Vic.*, 90, 175–194.
- Environment Conservation Council (2001), Box-ironbark forests & woodlands investigation: Final report, Melbourne, Vic., Australia.
- Foley, J. A., et al. (2005), Global consequences of land use, *Science*, 309, 570–574.
- Gee, G. W., and D. Hillel (1988), Groundwater recharge in arid regions: Review and critique of estimation methods, *Hydrol. Processes*, 2, 255–266.
- Gibbons, P., D. B. Lindenmayer, S. C. Barry, and M. T. Tanton (2002), Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management, *Biol. Conserv.*, 103, 1–12.
- González, E., M. González-Sanchis, A. Cabezas, F. A. Comin, and E. Muller (2010), Recent changes in the riparian forest of a large regulated Mediterranean river: Implications for management, *Environ. Manage.*, 45, 669–681.
- Gore, J. A. (1994), Hydrological change, in *The Rivers Handbook*, edited by P. Calow and G. E. Petts, pp. 33–54, Blackwell Science, Oxford.
- Harmon, M. E., et al. (1986), Ecology of coarse woody debris in temperate ecosystems, *Adv. Ecol. Res.*, 15, 133–302.
- Holland, K. L., I. D. Jolly, I. C. Overton, and G. R. Walker (2009), Analytical model of salinity risk from groundwater discharge in semi-arid, lowland floodplains, *Hydrol. Processes*, 23, 3428–3439.
- Horner, G., P. J. Baker, R. Mac Nally, S. C. Cunningham, J. R. Thomson, and F. Hamilton (2009), Regeneration and mortality of floodplain forests subjected to a drying climate and water extraction, *Global Change Biol.*, 15, 2176–2186.
- Horner, G., P. J. Baker, R. Mac Nally, S. C. Cunningham, J. R. Thomson, and F. Hamilton (2010), Carbon and habitat benefits from thinning floodplain forests: Managing early stand structure makes a difference, *For. Ecol. Manage.*, 259, 286–293.
- Jacobs, M. R. (1955), *Growth Habits of the Eucalypts*, 262 pp., For. Timber Bur., Commonw. Aust., Canberra, ACT, Australia.
- Jansen, A., and A. I. Robertson (2001), Relationships between livestock management and the ecological condition of riparian habitats along an Australian floodplain river, *J. Appl. Ecol.*, 38, 63–75.
- Jolly, I. D. (1996), The effects of river management on the hydrology and hydroecology of arid and semi-arid floodplains, in *Floodplain processes*, edited by M. G. Anderson, et al., pp. 577–609, John Wiley, Chichester, N. Y.
- Kingsford, R. T. (2000), Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia, *Austral Ecol.*, 25, 109–127.
- Koenker, R. (2010), quantreg: Quantile regression, R package version 4.48, accessed 17 June 2010. (Available at <http://CRAN.R-project.org/package=quantreg>.)
- Lada, H., J. R. Thomson, R. Mac Nally, G. Horrocks, and A. C. Taylor (2007), Evaluating simultaneous impacts of three anthropogenic effects on a floodplain-dwelling marsupial *Antechinus flavipes*, *Biol. Conserv.*, 134, 527–536.
- Lada, H., R. Mac Nally, and A. C. Taylor (2008a), Responses of a carnivorous marsupial (*Antechinus flavipes*) to local habitat factors in two forest types, *J. Mammalogy*, 89, 398–407.
- Lada, H., R. Mac Nally, and A. C. Taylor (2008b), Phenotype and gene flow in a marsupial (*Antechinus flavipes*) in contrasting habitats, *Biol. J. Linnean Soc.*, 94, 303–314.
- Lada, H., J. R. Thomson, R. Mac Nally, and A. C. Taylor (2008c), Impacts of massive landscape change on a carnivorous marsupial in south-eastern Australia: Inferences from landscape genetics analysis, *J. Appl. Ecol.*, 45, 1732–1741.
- Lawrence, L. (2009), Australian rabbits are doing what comes naturally—Again, *Outlooks on Pest Manage.*, 21, 19–21.
- Mackay, N., and D. Eastburn (Eds.) (1990), *The Murray*, Murray-Darling Basin Comm., Canberra, ACT, Australia.

- Mac Nally, R. (2001), "Mesoscale" experimental investigation of the dependence of riparian fauna on floodplain coarse woody debris, *Ecol. Manage. Restor.*, 2, 147–149.
- Mac Nally, R. (2006), Longer-term responses to experimental manipulation of fallen timber on forest floors of floodplain forest in south-eastern Australia, *For. Ecol. Manage.*, 229, 155–160.
- Mac Nally, R., and G. Horrocks (2007), Inducing whole-assemblage change by experimental manipulation of habitat structure, *J. Anim. Ecol.*, 76, 643–650.
- Mac Nally, R., and G. Horrocks (2008), Longer-term responses of a floodplain-dwelling marsupial to experimental manipulation of fallen timber loads, *Basic Appl. Ecol.*, 9, 458–465.
- Mac Nally, R., and A. Parkinson (2005), Fallen timber loads on southern Murray-Darling basin floodplains: History, dynamics and the current state in Barmah-Millewa, *Proc. R. Soc. Vic.*, 117, 97–110.
- Mac Nally, R., A. Parkinson, G. Horrocks, and M. Young (2002a), Current loads of coarse woody debris on southeastern Australian floodplains: Evaluation of change and implications for restoration, *Restor. Ecol.*, 10, 627–635.
- Mac Nally, R., G. Horrocks, and L. Pettifer (2002b), Experimental evidence for beneficial effects of fallen timber in forests, *Ecol. Appl.*, 12, 1588–1594.
- Mac Nally, R., A. F. Bennett, J. R. Thomson, J. Q. Radford, G. Unmack, G. Horrocks, and P. A. Vesik (2009), Collapse of an avifauna: Climate change appears to exacerbate habitat loss and degradation, *Div. Distrib.*, 15, 720–730.
- Maheshwari, B. L., K. F. Walker, and T. A. McMahon (1995), Effects of regulation on the flow regime of the River Murray, Australia, *Reg. Rivers Res. Manage.*, 10, 15–38.
- McAlpine, C. A., J. Syktus, J. G. Ryan, R. C. Deo, G. M. McKeon, H. A. McGowan, and S. R. Phinn (2009), A continent under stress: Interactions, feedbacks and risks associated with impact of modified land cover on Australia's climate, *Global Change Biol.*, 15, 2206–2223.
- McGinness, H. M., A. D. Arthur, and J. R. W. Reid (2010), Woodland bird declines in the Murray-Darling Basin: Are there links with floodplain change?, *Rangeland J.*, 32, 315–327.
- Murray-Darling Basin Commission (2005), Survey of river red gum and black box health along the River Murray in New South Wales, Victoria and South Australia—2004, report, Murray-Darling Basin Comm., Canberra, ACT, Australia.
- Murray-Darling Basin Ministerial Council (1999), The salinity audit of the Murray-Darling Basin: A 100-year perspective, Canberra, ACT, Australia.
- Merritt, D. M., and D. J. Cooper (2000), Riparian vegetation and channel change in response to river regulation: A comparative study of regulated and unregulated streams in the Green River Basin, USA, *Regul. Rivers Res. Manage.*, 16, 543–564.
- Merritt, D. M., and N. L. R. Poff (2010), Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers, *Ecol. Appl.*, 20, 135–152.
- Morgan, D. G., and P. Pegler (2010), Managing a kangaroo population by culling to simulate predation: The Wyperfeld trial, in *The Biology of Kangaroos, Wallabies and Rat-Kangaroos*, edited by D. Coulson and M. Eldridge, pp. 349–360, Commonw. Sci. Ind. Res. Organ. Publ., Melbourne, Vic., Australia.
- Natural Resources Commission (NRC) (2009a), Riverina bioregion regional forest assessment: River red gums and woodland forests, final assessment report, 336 pp., Nat. Resour. Comm., Sydney, N.S.W.
- Natural Resources Commission (NRC) (2009b), Riverina bioregion regional forest assessment: River red gums and woodland forests, recommendations report, 52 pp., Nat. Resour. Comm., Sydney, N.S.W.
- Overton, I. C., I. D. Jolly, P. G. Slavich, M. M. Lewis, and G. R. Walker (2006), Modelling vegetation health from the interaction of saline groundwater and flooding on the Chowilla floodplain, South Australia, *Aust. J. Bot.*, 54, 207–220.
- Page, K., A. Read, P. Frazier, and N. Mount (2005), The effect of altered flow regime on the frequency and duration of bankfull discharge: Murrumbidgee River, Australia, *River Res. Appl.*, 21, 567–578.
- Palmer, M. A., C. A. R. Liermann, C. Nilsson, M. Flörke, J. Alcamo, P. S. Lake, and N. Bond (2008), Climate change and the world's river basins: Anticipating management options, *Frontiers Ecol. Environ.*, 6, 81–89.
- Parolin, P., et al. (2004), Central Amazonian floodplain forests: Tree adaptations in a pulsing system, *Bot. Rev.*, 70, 357–380.
- Petratis, P. S., R. E. Latham, and R. A. Niesenbaum (1989), The maintenance of species diversity by disturbance, *Q. Rev. Biol.*, 64, 393–418.
- Raftery, A. E., D. Madigan, and J. A. Hoeting (1997), Bayesian model averaging for linear regression models, *J. Am. Stat. Assoc.*, 92, 179–191.
- Robertson, A. I., and R. W. Rowling (2000), Effects of livestock on riparian zone vegetation in an Australian dryland river, *Regul. Rivers: Res. Manage.*, 16, 527–541.
- Robinson, R. (1997), Dynamics of coarse woody debris in floodplain forests: Impact of forest management and flood frequency, B.S. thesis, Charles Stuart Univ., N.S.W., Australia.
- Sabo, J. L., et al. (2005), Riparian zones increase regional species richness by harboring different, not more, species, *Ecology*, 86, 56–62.
- Stromberg, J. C., S. J. Lite, and M. D. Dixon (2010), Effects of stream flow patterns on riparian vegetation of a semiarid river: Implications for a changing climate, *River Res. Appl.*, 26, 712–729.
- Tockner, K., and J. A. Stanford (2002), Riverine flood plains: Present state and future trends, *Environ. Conserv.*, 29, 308–330.
- Vaughan, I. P., M. Diamond, A. M. Gurnell, K. A. Hall, A. Jenkins, N. J. Milner, L. A. Naylor, D. A. Sear, G. Woodward, and S. J. Ormerod (2009), Integrating ecology with hydromorphology: A priority for river science and management, *Aquat. Conserv. Mar. Freshwater Ecosys.*, 19, 113–125.
- Vesik, P. A., R. Nolan, J. R. Thomson, J. W. Dorrrough, and R. Mac Nally (2008), Time lags in provision of habitat resources through revegetation, *Biol. Conserv.*, 141, 174–186.
- Victorian Environmental Assessment Council (VEAC) (2008), River red gum forests investigation: Final report, 208 pp., Melbourne, Vic., Australia.
- Walker, J., F. Bullen, and B. G. Williams (1993), Ecohydrological changes in the Murray-Darling Basin: 1. The number of trees cleared over two centuries, *J. Appl. Ecol.*, 30, 265–273.

P. J. Baker, S. C. Cunningham, G. J. Horner, R. Mac Nally, and J. R. Thomson, Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Bldg. 18, Clayton, Vic 3800, Australia. (Ralph.MacNally@monash.edu)