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Influence of Habitat Variability on Macroinvertebrate Biodiversity in River Red Gum Eucalyptus camaldulensis Floodplain Forest Andrea Alleyne Ballinger (B.Sc. Hons.) School of Biological Sciences Monash University December 2003

> A thesis submitted according to the requirements for the Degree of Doctor of Philosophy at Monash University, Victoria, Australia.

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Figure 6.4. Changes in mean (\pm SE) abundance and mean (\pm SE) species richness of
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Chapter Seven
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nean (\pm SE) abundance and mean (\pm SE) species richness of
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Abstract

Floodplains are dynamic ecotones that switch between aquatic and terrestrial phases. Variation in inundation patterns across the floodplain produces a mosaic of habitat patches. Flooding is regarded widely as a perturbation that acts over a discrete period. This has led to treatment of the aquatic phase and terrestrial phase as disconnected and has failed to recognize the contribution of habitat structure to diversity. Moreover, little is known about the time scales over which flooding influences biota. This thesis examines the effects of both habitat spatial structure and flooding on macroinvertebrate biodiversity in south-eastern Australian river red gum *Eucalyptus camaldulensis* floodplain forest. By considering the contributions of these factors throughout the entire flooding cycle and for 2 yr after emersion, a more comprehensive understanding of the ecology of this floodplain forest is developed.

The presence of fallen timber generates spatial complexity in any forest-floor habitat. River red gum forests have suffered a human-induced reduction in fallen-timber loads with many impacts on biodiversity. I sampled logs to characterize the invertebrate fauna at various stages in the flood cycle. The log fauna was found to switch rapidly between aquatic and terrestrial species, suggesting a high level of tolerance to flooding in the terrestrial fauna. Aquatic dipteran larvae colonized the logs within two weeks of immersion and, within four weeks of floodwaters receding, the structure of terrestrial invertebrate assemblages was similar to that of logs which had not been inundated for two years. Flood history and the decay stage of logs influenced the fauna in different ways but, overall, the log fauna was species poor and consisted of habitat generalists. However, fallen timber promoted biodiversity of forest-floor invertebrates at small spatial scales (5 m around logs), possibly due to litter accumulation against logs. This relationship did not hold at larger spatial scales (0.25 ha sites). Therefore, structural elements of habitat and interactions between these elements and flooding influenced the biota, but the relative importance of the processes appears to be scale dependent.

Ground-active invertebrates were surveyed before and for 2 yr following a major flood to establish their short- and long-term responses to flooding. Areas of forest floor that experienced extended inundation were colonized by hydrophilic ground beetles (Coleoptera: Carabidae) and wolf spiders (Araneae: Lycosidae), substantially increasing ground-active invertebrate biomass in the short-term. Potential sources of these colonists included the edges of river channels and temporary wetlands. Flooding was associated with sustained greater species richness of beetles. Ant abundance and species richness and the abundance of ant-eating spiders (Araneae: Zodariidae) were reduced in flood-prone areas. However, these gradients existed before the flood and are likely to have resulted from changes in habitat structure associated with long-term variability in localized flood patterns.

The role of arboreal refugia in the survival of flightless arthropods during flooding was examined. Although facultatively arboreal spiders were numerically dominant in forestfloor assemblages, little evidence was found for widespread movement of ground-active spiders into arboreal refugia during flooding. In contrast, use of arboreal refugia was linked to persistence of a few species of ground-nesting ants in flood-prone areas. Highly developed flood-survival strategies are not prevalent in the invertebrates of river red gum floodplains, reflecting the large spatio-temporal variability in the flood regime and the geologically recent formation of the forests.

Despite the canopy being composed solely of river red gum, assemblages of grounddwelling invertebrates experience river red gum forests as habitat mosaics in which structural characteristics are important promoters of biodiversity. Thus, rather than frequently 'resetting' successional trajectories, the main impact of flooding in river red gum forests appears to be maintenance of habitat differences that sustain the mosaic. Models of floodplain ecology (e.g. the Flood Pulse Concept) are applicable to terrestrial invertebrates in river red gum forests if the role of habitat structure is considered explicitly. Moreover, managed flooding needs to maintain the habitat mosaic to achieve conservation of floodplain biodiversity and the ecological processes performed by the biota.

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Statement of Originality

This thesis contains no material that that has been submitted for the award of any other degree or diploma in any university or other institution.

To the best of my knowledge, this thesis contains no material previously published or written by another person, except where due reference is made in the text.

Andrea Alleyne Ballinger

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Introduction

Australian river-floodplain systems have been subjected to extensive anthropogenic disturbance since European settlement. Flow regimes have been altered by extensive regulation and currently, there are over 430 large dams on Australian rivers (ANCOLD) 1990). As much as 80% of the fallen timber appears to have been stripped from the floodplain forests in south-eastern Australia (Mac Nally et al. 2002a). Such large-scale habitat change is likely to impact on floodplain biodiversity and ecological processes. Macroinvertebrates comprise a major component of the diversity in natural systems and influence many ecological processes, such as nutrient cycling (e.g. Folgarait 1998) and primary production (e.g. Schmitz 2003). Floodplain forests are recognized to support unique invertebrate assemblages (e.g. Adis 1981; Bonn et al. 2002) and fallen timber is an important element of the floodplain-forest habitat (Braccia and Batzer 2001). Understanding how the floodplain functions as habitat is a prerequisite for developing effective restoration strategies (Benke 2001). The effects of altered flood regimes and depleted fallen-timber loads on invertebrates in Australian floodplain forests largely are unknown.

This research addresses how Australian floodplain forests and microhabitats within floodplain forests, especially logs, provide permanent and transient habitat for both terrestrial and aquatic invertebrates. The effects of flooding on invertebrates are measured to decide how applicable models of floodplain ecology developed elsewhere are to south-eastern Australia, as well as the efficacy of managed flooding for promoting biodiversity. The role of fallen timber as habitat is assessed for terrestrial and aquatic invertebrates. From this, the likely impacts of fallen-timber removal are inferred. By integrating the role of fallen timber as habitat during both flood periods and dry periods, a more comprehensive understanding of the role of logs in promoting biodiversity on floodplains is attained than could be achieved by considering either phase in isolation

Ecology of floodplain forests

Riparian forests grow on the broad floodplains of many large, lowland rivers. Globally, wetland forests cover over 10^8 ha, much of which is riparian (Lugo *et al.* 1990). Riparian forests are dynamic habitats that alternate between an aquatic phase and a terrestrial phase as floods inundate the floodplain and subsequently recede (Junk et al. 1989; Junk 1997). Inundation often stimulates higher productivity relative to adjacent upland areas (Brinson 1990) owing to the availability of moisture and the importation of nutrient-rich sediment by floodwaters (Tockner and Stanford 2002).

General conceptual frameworks for floodplain ecology are only in the preliminary stages of development (Junk 1996). Even a widely accepted, fundamental definition of a floodplain has not been attained. Floodplains have been defined in terms of hydrology, geology, topography and ecological criteria (Tockner and Stanford 2002). Junk et al. (1989) contended that difficulties categorizing ephemeral, floodplain wetlands as either closed, lentic systems or open, lotic systems led to floodplains largely being omitted from classical limnology. Moreover, the long history of river regulation in developed counties has prevented study of floodplain ecological processes and propagated a perception of rivers as discrete, two-dimensional conduits running through the landscape (Bayley 1995; Ward and Tockner 2001). This paradigm is epitomized by thè River Continuum Concept (Vannote et al. 1980), which emphasizes the ecological importance of longitudinal, but not lateral, connectivity in rivers. The River Continuum Concept has limited applicability to large floodplain forests, where rivers typically flow in multiple, reticulated channels (Brown et al. 1997).

The alternation between aquatic phases and terrestrial phases creates high levels of heterogeneity in floodplain habitat. The ecology of the floodplain system cannot be fully understood by considering the terrestrial phase or the aquatic phase in isolation (Junk 1997). However, developing a conceptual framework for synthesis of the aquaticand terrestrial-phase ecology has proved difficult. One approach to integration has been to treat the floodplain as a transitional zone (ecotone) between the aquatic ecosystem and terrestrial ecosystem, rather than as a unique ecosystem in its own right (Naiman

and Décamps 1990; Gregory *et al.* 1991; Tockner and Stanford 2002). Inundation is considered to be a large-scale 'external' process that maintains the floodplain ecotone (Naiman and Décamps 1990). This model is useful for understanding the interactions between aquatic and terrestrial processes, but struggles to integrate 'internal' processes occurring in large floodplain forests.

Terrestrial ecologists typically have perceived flooding as a natural disturbance that 'resets' successional trajectories (e.g. Salo *et al.* 1986). The predominance of early-successional species on floodplains is considered evidence that classical disturbance theory is applicable to floodplains (e.g. Décamps 1993; Naiman and Décamps 1997; Bonn *et al.* 2002). Vogl (1980) likened the aquatic biota's flood-disturbance response to that of the terrestrial biota. However, Junk (1997) contended that regarding flooding as a disturbance, rather than as a generator of functionally important heterogeneity, is a misinterpretation of floodplain theory. Bayley (1995) asserted that the flood pulse is not a disturbance and that the prevention of floods by river regulation should instead be regarded as a disturbance.

These different views of flooding reflect problems of semantics and difficulties inherent in applying general principles to diverse systems. Vogl (1980) recognized the anthropomorphic and pejorative connotations of the term "disturbance" and proposed that floodplains be referred to instead as "perturbation-dependent ecosystems." Natural perturbations (disturbances) that are part of the evolutionary history of an ecosystem have a rejuvenating effect on biota and are essential to the 'well being' of the system (Vogl 1980; Whitford *et al.* 1999).

The current most influential theoretical framework for floodplain ecology, the Flood Pulse Concept (FPC) (Junk *et al.* 1989), originated with aquatic ecologists seeking to develop a more holistic model of river-floodplain function (cf. Ward 1989). Junk *et al.* (1989) used the extensive floodplain of the unregulated Amazon River as an exemplar to develop the Flood Pulse Concept. This model highlights the importance of over-bank flows in establishing lateral connectivity between the river channel and the floodplain, maintaining productivity and promoting biodiversity (Junk *et al.* 1989). The implications of these processes for diversity in large floodplain forests are scaledependent. Tockner *et al.* (2000) considered the stability of channels in floodplain forests to be associated with relatively low biodiversity at small spatial scales. At larger scales, floodplain forests have a mosaic structure and are characterized by high habitat heterogeneity and biodiversity (Harper *et al.* 1997; Tockner *et al.* 2000).

The flood pulse often is very regular in tropical river-floodplain systems and many unregulated temperate systems. The fauna in tropical floodplain forests, particularly Amazonian forests, has responded to the predictable and ancient flood regime by developing sophisticated behavioural and physiological adaptations to inundation (see for instance, Adis and Schubart 1984; Adis and Messner 1997; Höfer 1997; Adis and Junk 2002). In regulated, temperate systems, flood patterns tend to be less predictable, favouring more opportunistic floodplain species (Adis and Junk 2002). Flood patterns are most variable in arid and semi-arid regions due, in part, to the irregular cycling of the El Niño Southern Oscillation (Walker *et al.* 1995). Walker *et al.* (1995) contended that the Flood Pulse Concept is applicable to Australian riverine ecology if the emphasis on a highly predictable, seasonal flood pulse is relaxed and opportunistic, flexible life-history strategies are regarded as an adaptation to unpredictable variability. Tockner *et al.* (2000) subsequently expanded the FPC model to incorporate the less predictable flooding in temperate river-floodplain systems.

Processes and biota in floodplain habitats

Floodplains function as a buffering zone between the terrestrial ecosystem and the river channel. The riparian zone filters runoff, controlling the rates that nutrients enter rivers (see review by Gregory et al. 1991). During floods, large volumes of sediments are mobilized and may be deposited on the floodplain (Walling et al. 1996). Thus, flooding is considered to cause heightened exchange of nutrients and organic matter between the floodplain and the river channel (Tockner et al. 1999), although few data are available on lateral fluxes of carbon during the flood pulse (Robertson et al. 1999). Microbial activity in floodplain forests is increased by transitions between the terrestrial phase and aquatic phase, facilitating organic debris decomposition and nutrient cycling (Molles et al. 1998).

Floodplains are recognized to perform a variety of ecosystem services, but the capacity to perform these services is diminished by disruption of natural inundation cycles by river regulation. When regular flooding is suspended, leaching of salt from soils is reduced, resulting in increased salinity problems, such as the death of riparian vegetation (Jolly et al. 1993). Similarly, reduction in flooding has been implicated in decreased movement of floodplain carbon into rivers and the subsequent domination of in-channel carbon production by algae (Robertson et al. 1999).

In unregulated rivers and in regulated river-floodplain systems managed for environmental values, floodplains provide important habitat for numerous plants and animals. Fish (Saint-Paul et al. 2000; Bretschko and Waidbacher 2001) and water birds (Kingsford 2000) migrate to inundated floodplains to take advantage of the rich and unique floodplain food resources. Inundated floodplains also provide suitable breeding conditions for many species of fish (Hoberg et al. 2002), although King (2002) contended that Australian floodplains might be less important to native fish breeding than was thought previously (cf. Junk et al. 1989; Harris and Gerke 1994). Water birds have been shown to rely heavily on floodplain habitat for breeding (Kingsford and Thomas 1995; Kingsford 2000) and to respond to river regulation practices (Briggs et al. 1997; Briggs and Thorton 1999). Temporary floodplain wetlands also attract

numerous terrestrial bird species (Kingsford 2000; Parkinson et al. 2002). Semiarboreal small mammals appear best able to exploit the floodplain habitat (Andersen et al. 2000).

The importance of flood regimes to aquatic-invertebrate biodiversity in floodplain wetlands has been demonstrated repeatedly (Timms and Boulton 2001; Hillman and Quinn 2002; Sheldon et al. 2002). In contrast, terrestrial arthropods largely have been ignored as a component of riparian ecosystems, despite their numerical dominance and diversity (Ellis et al. 2001). The small number of studies, together with the diversity of terrestrial invertebrates, has made identifying general patterns difficult. For instance, species richness of terrestrial taxa has been found to decline with increased flood frequency (Uetz et al. 1979), reach a maximum at intermediate flood frequency (Bell et al. 1999) and/or to be insensitive to flooding (Ellis et al. 1999). The strength of flood response varies between taxa. Beetles are very responsive to flood regime, whereas spiders respond more to structural features of the habitat (Bonn et al. 2002). Many of the generalist wetland spiders also are found on disturbed dry sites (Bell et al. 1999; Bonn et al. 2002). Van Helsdingen (1996) suggested that there is "no typical floodplain spider community." However, flood-prone sites are important habitat for specialist hydrophilic predators, including spiders that are adept at huntering on the interface between land and water (Greenwood et al. 1995; Bonn et al. 2002). Terrestrial floodplain invertebrates have been disregarded in Australian research (but see Framenau et al. 2002 and Meeson et al. 2002).

Most research on floodplain arthropods has been conducted in areas with moderate to high rainfall. Ellis et al. (2001) found that the composition of assemblages of riparian arthropods was affected by flood regime in arid, southern USA. Wenninger and Fagan (2000) demonstrated that riparian spiders in deserts were water-limited. If rainfall has a moderating influence, the contrast between invertebrate assemblages at regularly flooded and drier sites might be greatest in xeric regions.

Many studies of floodplain invertebrates have only sampled fauna on the ground or in the water column and hence, knowledge of the ecological function of different microhabitats within floodplains is limited. For instance, Benke (2001) demonstrated that the substrate at the bottom of emphemeral floodplain wetlands and logs within the

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river channel both support high biomass of aquatic invertebrates, but he did not sample logs on the floodplain. The role of fallen timber as habitat has been studied predominantly in wet, temperate forests where fallen timber has been shown to provide food, shelter and breeding sites to a diverse range of terrestrial organisms (e.g. Harmon et al. 1986; Schiegg 2000).

In river channels, fallen timber is a solid substrate in an otherwise unstable environment and, therefore, provides anchorage and oviposition sites for aquatic invertebrates, as well as refuge from drift and predation (see review by Hoffman and Hering 2000). Submerged logs on floodplains develop biofilms, which are thought to be an important food resource for grazing invertebrates (Scholtz and Boon 1993). However, Braccia and Batzer (2001) found that invertebrate density was greater on floating wood compared with submerged wood on an inundated floodplain, partially as a result of terrestrial invertebrates seeking refuge on floating wood. There does not appear to be any Australian studies that have integrated the role of logs on floodplains as habitat across flood and dry periods.

River red gum floodplain forests of the Murray-Darling Basin

Over 10⁶ km², or nearly 14% of Australia's land area, forms the catchment of Murray-Darling river system (Walker 1986). The Murray River is the principal river in the system. The prevailing climatic regime in the Murray-Darling Basin is semi-arid, but approximately half of Australia's primary agricultural production comes from the Murray-Darling Basin (Walker 1986). Approximately 60% of the annual flow of the Murray River is diverted to support agricultural production (Close 1990). Ecological problems associated with farming practices in the Murray-Darling Basin are becoming increasingly apparent and include rising salinity, eutrophication and changes to floodplain biota, particularly the floodplain forests.

The river red gum Eucalyptus camaldulensis Dehnhardt (Myrtaceae) is synonymous with riparian zones in lowland Australia. The river red gum is the most widely naturally

Access to river water, either directly as floodwater or as groundwater, sustains a higher growth rate in river red gum forests than rainfall alone (Dexter 1978). River red gum forests are highly productive areas within regions where water is scarce and productivity generally is low. Consequently, these forests are recognized as important refugia for biodiversity in semi-arid Australia (Morton et al. 1995). Typically, humans disrupt natural systems by multiple mechanisms and river red gum forests are no exception. Timber harvesting, firewood collection and stock grazing all occur in river red gum folests, altering the age structure of the trees and the characteristics of the ground layer. Furthermore, natural flood regimes have been altered by river regulation, changing forest growth and recruitment patterns.

distributed of all the *Eucalyptus* species, extending from Melbourne in the south-east of the continent to the Kimberly Ranges in the north-west (Jacobs 1955; Boland et al. 1984). For much of its range, particularly the arid central regions of Australia, river red gum has a serpentine distribution, tracing the margins of temporary and permanent waterways (Boland et al. 1984). In the south-east of the continent, river red gum forms monospecific open forests on the extensive floodplains of the Murray-Darling river system. Average tree species richness is 8.3 for floodplain forests across Europe and the Americas (Brinson 1990), so river red gum forests are unusual in containing pure stands of a single species.

Barmah-Millewa Forest—an Australian floodplain forest

Barmah-Millewa Forest (centred on $35^{\circ}55$ 'S $145^{\circ}08$ 'E) forms the world's largest nonplantation stand of river red gum (Fig. 1.1). The forest straddles the Murray River, which forms the bedder between two sta Victoria and New South Wales. Australian forests are under the jurisdiction of state governments and consequently, the forest often is c sidered as two distinct units. All fieldwork for this study was undertaken in the Victorian portion of the forest, referred to as Barmah Forest. Barmah Forest comprises Barmah State Forest (21 600 ha) and Barmah State Park (7 900 ha). The sole distinction between Barmah State Forest and Barmah State Park is legistlative because the two areas are contiguous and have identical historic and current management regimes (Dept. Conservation and Environment 1992). Consequently, they simply are referred to as Barmah Forest throughout this thesis.

In contrast to Amazonian floodplain forests, river red gum floodplain forests are geologically recent. Climatic conditions on the Murray-River floodplain are thought to have only become tenable for tree growth 13 000–10 000 yr BP, with the first abundant charcoal remains in the region dated at 8090 yr BP (Bowler and Harford 1966). Suitable hydrological conditions for the formation of Barmah Forest resulted from the uplifting of the Cadell Tilt Block (Fault) 20 000 yr BP creating a barrier to the westward progress of the Murray River (Bowler and Harford 1966; Currey and Dole 1978; Silvers 1993). The Murray River eventually broke through to the south of the block about 7000 yr BP (Bowler and Harford 1966), but the channel remains narrow in the region known as the Barmah Choke. Because of the reduced channel capacity, high flows breech the banks and inundate the forest. Elevations within the forest differ by only 1–2 m, with the exception of sand hills /Dexter 1978). Hence, floodwaters form extensive sheets across the forest floor. Floodwaters typically move very slowly through Barmah Forest and rejoin the main river channel downstream of the forest.

Under natural conditions. floods in Barmah Forest resulted from winter rainfall and spring snowmelt in upstream catchments (Dexter *et al.* 1986; Silvers 1993). Flooding turns the forest into a temporary wetland that supports a diverse array of water birds,

amphibians and reptiles (Chesterfield *et al.* 1984). In recognition of its significance as water bird breeding habitat, Barmah Forest is categorized as a Wetland of International Importance by the Ramsar Convention, an intergovernmental treaty dedicated to wetland conservation (Holmes 2001).

The 29 500 ha Barmah Forest contains 24 440 ha of monospecific stands of river red gum. The river red gum overstorey is absent from the most flood-prone areas of the forest. Rushland, consisting of closed tussocks of the giant rush Juncus ingens Wakefield occupies approximately 1.5% of forest area and moira grasslands Pseudoraphis spinescens (R.Br.) cover a further 5% (Chesterfield 1986). The extent of forest rushlands and grasslands has been reduced substantially since 1840 by historic grazing pressure and by changes in fire and flood regimes (Chesterfield 1986). The moira grasslands continue to be invaded by river red gum (Bren 1992). River red gum also is absent from ridges of sand hills and from the margins of the forest that are flooded very rarely (Chesterfield 1986). These areas have mixed open stands of grey box Eucalyptus microcarpa (Maiden), yellow box Eucalyptus mellidora Cunn. and black box Eucalyptus largiflorens Muell.. The understorey is dominated by monocotyledons capable of rapid vegetative growth, interrupted by periods of dormancy when conditions are unfavourable (e.g. wallaby grasses Danthonia species and warrego summer grass Paspalidium jubiflorum (Trin.)). The composition of the grassy understorey varies throughout the forest, largely in response to flood regime.

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History of human impacts on Barmah Forest

Floodwaters sustain a level of productivity in Barmah Forest that is greater than for the surrounding sub-humid landscape. This long has made the forest attractive to humans. Before European settlement, the central Murray area is thought to have supported high densities of aboriginal people relative to other, less productive regions (Webb 1984; Lyons 1988). Aborigines are estimated to have set fires in the forest as frequently as once every five years (Lyons 1988). The laminar bark of river red gum renders it vulnerable to fire. The frequent burning is considered to have maintained a woodland structure (Chesterfield 1986), described by the squatter Edward Curr as "open, grassy, forest land" with "a very pleasant aspect of mixed Australian and semi-tropical character" [Curr 1968 (Facsimile of the 1883 publication)]. However, Fahey (1986) quotes official reports from 1869 and 1870 stating that the river red gums were "so dense that the eye can penetrate only a little way into the forest," and that there were "80 to 100 trees per acre." Probably, stand density always varied throughout the forest. Attempts to use the pollen record preserved in sediments to infer changes in the density of river red gums since European settlement have not identified any consistent patterns across sites (Kenyon and Rutherfurd 1999; Kenyon 2001).

European impacts on the ecology of Barmah Forest commenced in the 1840s with squatters grazing stock in the forest (Fahey 1986). Grazing has been associated with understorey changes in the forest, including the decline of more palatable species and the introduction of weeds (Chesterfield *et al.* 1984). Jacobs (1955) noted that grazing by cattle, horses and rabbits can limit river red gum regeneration. Robertson and Rowling (2000) found stocking rates of 12 dry sheep equivalents ha⁻¹ yr⁻¹ to substantially reduce *Eucalyptus* recruitment in riparian zones along the Murrumbidgee River and suggested that livestock impacts might override any beneficial effects of flooding. However, at stocking rates of 2000 head of cattle in 19 425 ha of forest, Dexter (1978) found grazing rarely to impact on seedling establishment. Currently there are ca 1400 cattle grazing Barmah Forest (John Kneebone, Head Ranger Barmah Forest, pers. comm.).

Commercial timber harvesting began in Barmah Forest with the opening of the first sawmill in 1863–1864 (Fahey 1986). Timber harvesting continues in the forest today, although at much reduced levels with ca 10 000 t harvested annually (John Kneebone, Head Ranger Barmah Forest, pers. comm.). Firewood extraction also continues to occur. Eighty percent of the firewood sold by Victorian merchants is extracted from river red gum forest (Driscoll *et al.* 2000). Fallen timber and off-cuts from timber harvesting are taken. Mac Nally *et al.* (2002a) calculated that firewood collection and timber harvesting practices have reduced fallen-timber volumes in Barmah Forest to approximately 20% of pre-European settlement levels. Increased loads of fallen river red gum timber are associated with greater local activity of an insectivorous bird, the brown treecreeper *Climacteris picumnus* Temminck (Mac Nally *et al.* 2002b), and an insectivorous marsupial, the yellow-footed antechinus, *Antechinus flavipes* (Waterhouse) (Mac Nally *et al.* 2001).

In 1934 major regulation of the Murray River began with the opening of the Hume Dam at Albury (36°30'S 146° 30'E), ca 300 km upstream from Barmah Forest. Regulation increased flooding in summer, when river levels are raised to supply irrigators. It quickly was realized that prolonged summer flooding was associated with tree deaths in low-lying areas (Incoll 1946; Fahey 1986). Installation of a network of water regulators on the influent channels commenced in the 1940s and has reduced the problem of excessive, extended summer flooding. However, the duration, frequency and extent of forest flooding are less than would occur naturally (Dexter *et al.* 1986; Bren 1987). Furthermore, the seasonality of flooding has shifted, with less winter and spring flooding and an increase in the frequency of small, brief summer floods (Dexter *et al.* 1986).

The link between flooding and enhanced silvicultural productivity long has been recognized (Boomsma 1950; Fahey 1986). Soon after the Hume Dam became operational, silviculturalists began lobbying for the irrigation of the river red gum forests to ameliorate the effects of river regulation (Incoll 1946). The 1990s saw a renaissance in Australian water management policy with the introduction of environmental flows. In 1993 the Murray Darling Basin Ministerial Council granted an Environmental Water Allocation of 100 GL per annum for flooding Barmah-Millewa Forest (Barmah-Millewa Forum 2001). Delivery of the Environmental Water

Allocation is contingent upon release triggers and guidelines; hence, a consistent amount of water is not delivered to the forest annually (Barmah-Millewa Forum 2001). Environmental Water Allocations were released in the forest in 1998 and 2000. The small 1998 release did not result in significant flooding, but the larger 2000 release of 341 GL inundated 85% of the Barmah Forest (Barmah-Millewa Forum 2001). Sufficient long-term records exist to enable the 'success' of the 2000 flood to be assessed in terms of water bird breeding events (Barmah-Millewa Forum 2001). However, for other taxa, little effort has been that to measure the benefits of Environmental Water Allocations, reflecting a nation-wide trend that threatens to undermine the political will for environmental flows (but see Reid et al. 2001).

This thesis examines how managed flooding and the presence of fallen timber maintain invertebrate diversity by generating habitat heterogeneity in floodplain forest. The role of fallen timber in promoting biodiversity is examined at the local and site scales for invertebrates living in logs and on the forest floor. The colonization sequence of fallen timber during transitions between the aquatic phase and the terrestrial phase is followed to determine the role of fallen timber as habitat for both aquatic and terrestrial biota, and to assess faunal tolerance of flood perturbation. Ground-active invertebrate assemblages were tracked for 2 yr after a major Environmental Water Allocation to identify the short-term and long-term effects of managed flooding on biodiversity. The prevalence of various strategies to survive both flood periods and dry periods is assessed and used to draw conclusions about the extent of specialization in Australian floodplain fauna. Last, the implications of the findings of this research for floodplainforest management are considered.

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Figure 1.1. Map of the study area (modified from a satellite photograph). The inset shows the position of Barmah Forest in Austalia.

CHAPTER TWO

THE ROLE OF HABITAT CHARACTERISTICS AND DISTURBANCE IN STRUCTURING INVERTEBRATE ASSEMBLAGES IN RIVER RED GUM EUCALYPTUS CAMALDULENSIS LOGS

Abstract

The effects of habitat structure and flood-perturbation on the structure of log-dwelling invertebrate assemblages was assessed in south-eastern Australian river red gum Eucalyptus camaldulensis floodplain forest. Logs were chosen as habitat because they maintain structural integrity throughout the flood cycle. The invertebrate fauna in river red gum logs was relatively depauperate, possibly reflecting the variable, sub-humid conditions on the floodplain. The abundance and species richness of invertebrates increased with the complexity and heterogeneity generated by decay; however, the composition of invertebrate assemblages was related to local flood regime. Frequent inundation appeared to maintain a highly flood-resilient fauna. The invertebrate successional sequence of logs was tracked though transitions between terrestrial fauna and aquatic fauna in a spring/summer flood cycle. Transition between the two faunae. was extremely rapid. Logs were colonized by aquatic invertebrates within 2 wk of being immersed by floodwaters. The composition of invertebrate assemblages in logs 4 wk after the recession of floodwaters closely resembled that of logs not flooded for 1-2yr. Therefore, the terrestrial invertebrate assemblage of logs in regularly inundated areas appears to be highly effective at utilizing external refugia. Moreover, the faunal dynamism highlights the need to consider the entire flood cycle when assessing the contribution of logs on floodplains to maintaining biodiversity.

Introduction

Relationships between habitat structure and biodiversity have been recognized for many decades (*sensu* Hart and Horwitz 1991). Habitat structure comprises habitat complexity, defined as how much habitat is in a given area, and habitat heterogeneity, defined as the variability of habitat in a given area (McCoy and Bell 1991). Greater habitat complexity provides organisms with more of the same resources, whereas habitat heterogeneity provides a greater variety of resources. Habitat complexity and heterogeneity frequently have been confounded in ecological studies (McCoy and Beli 1991), despite their importance to several mechanistic models of the species-area relationship (*sensu* Hart and Horwitz 1991; O'Connor 1991).

Recent studies have gone beyond simply correlating habitat structure with biodiversity to explore relationships between biodiversity and ecosystem processes. Aquatic ecologists have contended that habitat heterogeneity, measured at the scale of the stream bed, is highly effective at mitigating the impact of flood-disturbance on aquatic invertebrates (Lancaster and Hildrew 1993; Lancaster 1996; Lake 2000 and references therein). Greater habitat heterogeneity generally is considered to ameliorate the impacts of disturbance by providing biota with more refugia (i.e. habitat patches that remain intact throughout the disturbance because of their differing characteristics) (Sedell et al. 1990). Thus, habitat complexity confers resilience, here defined as the capacity of a biotic assemblage to return to its pre-disturbance state following displacement by disturbance (Palmer et al. 1995). Problematically, in-stream macroinvertebrate assemblages typically are not sampled during flood-disturbance. Passive or active movement into refugia is inferred from the distribution of invertebrates soon after the spate subsides (e.g. Robertson et al. 1995; Thomson 2002). Thus, it rarely is demonstrated that provision of refugia is the mechanism by which habitat heterogeneity confers resilience.

The faunal assemblages inside fallen timber in floodplain forests lend themselves to investigating the influence of habitat structure on biodiversity under both 'baseline' and disturbance conditions. Logs of different age classes provide different levels of structural intricacy, with older logs containing more extensive hollows. Thus, older logs may provide greater habitat complexity and heterogeneity and, therefore, may support a richer, more abundant fauna (*sensu* Harmon *et al.* 1986). O'Connor (1991) demonstrated that greater habitat heterogeneity was responsible for increased species richness of aquatic-invertebrate assemblages on logs in stream channels. O'Connor (1991) reasoned that measuring species evenness, rather than species richness, avoided confounding habitat complexity and habitat heterogeneity because species evenness is expected to increase with the variety, but not the abundance, of resources available.

Logs maintain structural integrity throughout the flood cycle, enabling the response to disturbance to be assessed independently of changes in habitat complexity. Moreover, inundation in floodplain forests is of comparatively low energy and long duration, allowing logs to be sampled during flooding. When submerged entirely in floodwater for a prolonged period, logs become waterlogged, obscuring the small-scale variability created by different levels of decay. At this point, sampling of logs will establish whether the terrestrial inhabitants have moved into external refugia or have drowned. (Movement into refugia is considered in Chapter Six.) Hence, in contrast to riffle habitats in streams, it is easy to demonstrate that submerged logs are uninhabitable to terrestrial invertebrates during flooding.

Most studies of invertebrates associated with logs have been conducted in forests that are characterized by relatively consistent environmental conditions, such as European and North American boreal forests (Ake *et al.* 1994; Nilsson and Baranowski 1997; Jonsson 1999; references in Stevens 1997). Under these conditions, invertebrates appear to have evolved very specialized habitat requirements and low dispersal capabilities, resulting in fine-scale patterns in habitat utilization. Schiegg (2000) demonstrated that for saproxylic (associated with dead wood) invertebrates in a stable habitat, population fragmentation occured at a highly localized scale through the isolation of single logs. In contrast, logs on floodplains are subject to high habitat variability created by the alternation between an aquatic phase and a terrestrial phase, favouring invertebrates with generalized life-history strategies and high mobility (*sensu* Adis and Junk 2002).

Flooding might be 'catastrophic' to populations of invertebrates in logs (*sensu* Adis and Junk 2002). Conversely, regular flooding might be needed to sustain both the terrestrial and aquatic floodplain fauna. Flooding promotes the activity of fungi and cellulose

decomposers, increasing the rate of mass loss of logs (Molles *et al.* 1998), and potentially augmenting the resources offered to invertebrates. The negative impacts of flood mitigation have been demonstrated for aquatic floodplain taxa, especially fish (e.g. Saint-Paul *et al.* 2000; Bretschko and Waidbacher 2001), but little research has considered effects on terrestrial invertebrates (Ellis *et al.* 2001). Moreover, floodplain ecology has been criticized for not integrating the aquatic phase and terrestrial phase (Junk 1997). By failing to sample floodplain habitat over the entire flood cycle, investigators underestimate the contribution of floodplains to sustaining biodiversity.

This study was undertaken on fallen timber in river red gum *Eucalyptus camaldulensis* Denhn. forest. River red gum forests occur on the floodplains of rivers in Australia. Since settlement by Europeans, these floodplain forests have been much altered. First, the ground-'ayer structure has been simplified by the removal of large amounts of fallen timber (Mac Nally and Parkinson 1999). Removal of fallen timber has been shown to affect native vertebrates in river red gum forest (Mac Nally *et al.* 2001). Second, river management has disrupted flood regimes, reducing both the frequency and extent of inundation (Bren 1987). Under natural flood regimes, frequent inundation creates high temporal variability in habitat conditions on the forest floor. Thus, reduction in flooding can be viewed as another form of habitat simplification with potential impacts on biodiversity.

Here, the responses of invertebrate fauna on the floodplain to habitat structure provided by the structural characteristics of fallen timber and to flood perturbation were investigated. I aimed to assess whether more decayed logs support greater densities and species richness of invertebrates and to explore the relative importance of habitat complexity and heterogeneity to species richness. I considered short-term (< 12 wk) and long-term (> 1 yr) impacts of flood disturbance on invertebrate assemblages to gauge faunal resilience to flooding and to determine if a flood-dependent fauna exists.

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Methods

Study area

This work was conducted in Barmah State Forest and Barmah State Paik on the Murray-River floodplain, in northern Victoria, Australia, about 215 km from Melbourne (35°55'S 145°08'E). Barmah Forest consists largely of monospecific stands of *Eucalyptus camaldulensis* with an understorey of grasses, sedges and rushes (Chesterfield 1986).

Sampling Protocol

Faunal changes associated with spatial complexity and flood reduction: 2001 sampling

In 2001, 68 sections of log ≈ 1 m in length, at varying decay stages, were collected from four sites throughout Barmah Forest. Two of the sites had not experienced flooding for many years. The other two sites had been inundated the previous austral spring/summer (2000-2001). One of the flood-prone sites was the area where the 2002 sampling was conducted and both transferred (20) and untransferred (17) logs were taken from that site in 2001 (see below explanation of 2002 sampling). Logs were chosen to be ≈ 0.12 m in diameter. Sections were extracted using a hand saw or chain saw. Log sections were immediately sealed in thick garbage bags for transport to the laboratory. Invertebrates under logs were collected with forceps and brushes.

Colonization trajectories over flood events: 2002 sampling

In May 2001, 100 logs of ≈ 1 m length and diameter ≈ 0.12 m were transferred from an area that had experienced prolonged inundatation in spring/summer 2000-2001 to one of the flood-prone study sites. The logs were chain sawn into 1-m lengths before

transportation. Only logs with low to medium-low levels of decay were chosen to reduce the likelihood of the logs disintegrating during flooding and transportation. The logs were anchored to prevent movement during flooding and to make the submerged logs easy to locate. The anchoring-structure consisted of two rows of star pickets hammered into the forest floor at 2 m intervals, with a line of fencing wire running along each row 0.12 m above the forest floor (Fig. 2.1). Eighty of the logs were placed under the wire and separately anchored to each wire with a fencing staple. The remaining 20 logs were stacked nearby.

I had intended to retrieve the logs for sampling when the site flooded in spring 2001. A total of twenty logs were serially retrieved and replaced with logs from the nearby pile throughout austral spring/summer 2001–2002. The transferred logs were not inundated in 2001, necessitating extension of the sampling regime to spring/summer 2002–2003. However, the collection of the 2001–2002 data was important to demonstrate, among other things, that the fauna in the transferred logs matched the fauna in the fallen timber already at that site.

In late-October 2002, the transferred logs were flooded. Logs were retrieved after 2 wk and 6 wk of submersion. Floodwaters receded in late December 2002, and logs were sampled at 1 wk and 4 wk after emersion. The difficulty of working in floodwaters made replacement sampling impossible; however, only a small proportion (17) of the total logs were removed. Contemporaneously, logs of the same size were collected from areas of the site that were not inundated.

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Destructive sampling technique

On being returned to the laboratory, logs were weighed, measured and the state of decay assessed. Logs then were hand-searched for invertebrates, using chisels to prise off loose wood and forceps and paintbrushes to collect specimens. Because river red gum timber is extremely hard, a band saw was used to section logs into 0.05 m lengths, which then were re-examined for invertebrates. It often was difficult to extract all individuals from ant and termite nests. However, slowly submerging small pieces of log in water was an effective way to cause nest-evacuation and to facilitate collection. Adult specimens were identified to the highest practicable taxonomic level (generally genus for ants and beetles, family for spiders) and expert taxonomic assistance was sought to identify the more common taxa (see acknowledgements). All juvenile specimens of terrestrial species were excluded from consideration because treating larvae and adults as separate morphospecies would lead to overestimation of diversity. Keys are not widely available for many immature terrestrial invertebrates in Australia. For consistency, ant eggs/larvae/pupae also were excluded from analysis, even though they clearly belonged to the same species as adult workers in the nest. However, larvae of aquatic taxa were included in the analysis because they could be accurately classified due to the availability of extensive keys.

The characteristics used to assign logs to decay classes are given in Table 2.1. Logs from dry areas generally only had limited rot, even when extensively hollowed. Extent of hollows was taken as the primary characteristic for assigning logs to decay classes, although cracks in the surface of the log also increased structural complexity in the more advanced decay stages. The extent of hollows often was not evident until logs were broken, so the number of logs in each decay class is uneven.

Analyses

program.

sampling

Two-factor ANOVAs were run on (1) the abundance and; (2) the species richness of invertebrates per log in 2001. Factors were log decay class (0-5), and whether the area the log was taken from had been inundated the previous year, i.e. spring/summer 2000-2001.

Because the fauna was depauperate and social insects comprised the overwhelming majority of individuals caught, species evenness indices could not be generated for many of the logs. Consequently, it was not feasible to use species evenness to separate the effects of habitat complexity and habitat heterogeneity (cf. O'Connor 1991).

The structure of invertebrate assemblages was compared between logs of different decay classes. Bray-Curtis similarity matrices were generated for the 2001 destructivesampling data. Destructive-sampling data were square-root transformed to reduce the influence of very abundant species. Prior to conducting a two-way crossed ANOSIM, the decay classes were pooled from six into three groups (low, medium and extensive decay) to increase the number of logs in each group, due to limited resolution and permutations in ANOSIM. A two-way crossed ANOSIM then was performed with decay class and inundation history (flooded or not flooded in 2000) as the factors. SIMPER analysis was performed on the data to identify influential species contributing to the differences identified by the ANOSIM.

Analyses of variance (ANOVA) were performed using SYSTAT (Version 10, SPSS Inc. 2000). Analyses of similarities (ANOSIM). similarity percentage (SIMPER) analyses and generation of the non-metric, multidimensional scaling plot were conducted with PRIMER (Version 5, Clarke and Gorley 2001) statistical computer

Faunal changes associated with structural complexity and flood disturbance: 2001

Colonization trajectories over flood events: 2002 sampling

To check that the fauna in the transferred logs had equilibrated with the fallen-timber fauna at the site, ANOSIM (square-root transformed data) was run on the 2001 speciesby-log data with site-of-origin as the grouping factor. Only untransferred logs with a decay classification of ≤ 3 were included because the transferred logs had been selected to have low to low-moderate levels of decay.

One-factor ANOVAs then were calculated with the dependent variables being (1) the abundance and; (2) the species richness of invertebrates per log in 2002. Stage in the wetting and drying cycle was the between-group factor for both ANOVAs and had five levels (2 wk immersed, 6 wk immersed, 1 wk emersed, 4 wk emersed, unflooded logs from the same site). Tukey's HSD test was used to make pairwise comparisons between (1) abundance and; (2) species richness of log fauna at different stages in the wetting and drying cycle.

To compare the composition of invertebrate assemblages between different stages in the flood cycle, a Bray-Curtis similarity matrix was generated from the species-by-log data for both the 2002 data and the 2001 data from the two flood-prone sites. A one-factor ANOSIM then was performed with the matrix partitioned into the following groups: 2 wk immersion, 6 wk immersion, 2 wk emersion, 4 wk emersion, unflooded logs at treatment site 2002, logs collected at flood-prone sites in November and December 2001. A non-metric multidimensional scaling plot was generated to represent the faunal similarities visually.

Results

Faunal changes associated sampling

In 2001, 54 morphospecies of adult invertebrates were recovered from logs by destructive sampling, including ten ants (Hymenoptera: Formicidae), one termite Coptotermes acinaciformis (Froggatt) (Isoptera: Rhinotermitidae), 20 spiders (Araneae) and 13 beetles (Coleoptera) (Appendix 2.1). Ants and termites numerically were dominant, comprising 20 830 of the 21 004 specimens recovered (99% of individuals). The abundance and species richness of invertebrates per log increased with the decay class/spatial complexity of logs (Table 2.2, Fig. 2.2). Species richness averaged < 1.5 morphospecies per log in the three lowest decay classes and reached a maximum of 4.6 morphospecies in extensively decayed logs (Fig. 2.2b). Whether a log had been inundated the previous spring/summer did not influence abundance or species richness overall. However, the interaction between decay class and flood history was significant for both abundance and species richness (Table 2.2), indicating that flood-response was dependent on the decay-state of the log. Composition of invertebrate assemblages was not related to the decay class/spatial complexity of the wood (Table 2.3). Logs subject to flooding the previous year had significantly different faunal composition to logs collected from unflooded areas (Table 2.3).

Differences in abundance of the termite *Coptotermes acinaciformis* and an ant *Doleromyrma* sp. (*darwinian*a group) accounted for much of this variation in assemblage structure because both morphospecies were essentially absent from flood-prone areas (Table 2.4).

Colonization trajectories over flood events: 2002 sampling

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Faunal changes associated with structural complexity and flood disturbance: 2001

The results of that ANOSIM did not provide compelling evidence that the fauna in transferred logs had equilibrated with the fauna in surrounding (untransferred) fallen timber in 2001 (R = 0.077, $P \approx 0.053$). Unfortunately, the equilibration could not be retested in 2002 because the transferred logs were submerged before the first 2002 samples were taken. However, the very low *R*-value indicates that faunal variability between logs transferred into the study area and logs from the study area was only about 8% greater than faunal variability within each group of logs. Thus, it is reasonable to assume that the transferred logs were functioning as 'normal' invertebrate habitat when the flood commenced. Furthermore, the marked faunal change associated with flooding and the subsequent re-colonization with terrestrial fauna render concerns about subtleties in faunal equilibrium biologically relatively minor.

Both the abundance and species richness of the invertebrate fauna changed as logs moved through different stages in the wetting and drying cycle (Table 2.5; Fig. 2.3a and b). The colonization of the flooded, transferred logs by aquatic invertebrates was rapid. Larval Diptera already had colonized the log substrate when the first samples were taken 2 wk after inundation commenced. Mean abundance of individuals per log was significantly greater in logs that had been immersed for 6 wk compared with unflooded logs or logs which had been emersed for 4 wk (Fig. 2.3a). The diversity of the aquatic fauna that colonized the logs was low—only eight species of aquatic invertebrates were recovered from logs, in total (Fig. 2.3b). After 6 wk emersion, mean species richness per log was 3.6 ± 0.7 . Larvae of a *Kiefferulus* species (Diptera: Chironomidae) numerically dominated the fauna, comprising 97.5% of all individuals collected at 6 wk inundation. Animals were found almost exclusively on the exterior surface of the logs. If log surface area is approximated by a cylinder of length 1.0 m and radius 0.06 m, the mean density of the *Kiefferulus* species was $1190 \pm 374 \text{ m}^2$ after 6 wk immersion.

The composition of assemblages followed a serial successional trajectory, with faunal similarities at each sampling time being more similar than between sampling times (Table 2.6, Fig. 2.4). Recolonization of the logs by terrestrial fauna following floodwater subsidence was rapid. After 4 wk emersion, the composition of the faunal assemblages was not different from logs that had not flooded that year (Table 2.6, Fig. 2.4). Nor was the fauna after 4 wk emersion distinguishable from the fauna in logs collected from flood-prone sites in 2001 (Table 2.6, Fig. 2.4).

Discussion

The fauna in river red gum logs

The importance of logs as habitat for invertebrates has been documented well in the Northern Hemisphere (Harmon *et al.* 1986; Stevens 1997). Invertebrates use fallen timber for shelter, as sites for breeding, and as direct or indirect sources of food (Harmon *et al.* 1986). Few Australian studies have looked specifically at how logs provide habitat. The conservation value of rotting logs has been demonstrated for a small number of Australian species, including a saproxylic stag beetle (Meggs and Taylor 1999) and an onychorphoran (Barclay *et al.* 2000).

The fauna inside river red gum logs in the three earliest decay classes averaged ≈ 1.5 morphospecies per log (Fig. 2.2). The fauna in river red gum logs was depauperate compared to fauna in logs from other species. For instance, Fager (1968) found a median of 48 species per 0.075 m \times 0.70 m piece of decaying oak *Quercus robur* L. wood. The termite *Coptotermes acinaciformis* was the only known obligate saproxylic species that I recovered from river red gum logs. The dearth of obligate saproxylic species was expected because of the high temporal variability in environmental conditions in floodplain forests. Although specialized to eat wood, *C. acinaciformis* displays plastic habitat requirements. It tolerates a wide range of climatic conditions, consumes wood from numerous species and displays considerable variation in nesting habitats, including the ability to nest in trees (Gay and Calaby 1970). The adaptability of *C. acinaciformis* probably facilitates its persistence in the floodplain environment. Eight morphospecies of ant were found nesting in logs, but it is not known if rotting wood is their only nesting substrate.

The small number of saproxylic species in river red gum forest contrasts with the rich invertebrate fauna associated with fallen timber in many northern-hemisphere forests. For instance, in a Swiss beech *Fagus sylvatica* L. forest there were > 500 saproxylic dipteran species and > 150 saproxylic coleopterans (Schiegg 2000). Many saproxylic insects rely, directly or indirectly, on wood-decaying fungi. Wood is largely resistant to

enzymatic degradation, is low in nitrogen and deficient in essential vitamins (Beaver 1989). Fungi decompose cellulose and lignin into organic chemicals that insects can assimilate, as well as concentrating nitrogen and synthesizing essential nutrients (Beaver 1989). The low rainfall (386 mm yr⁻¹) in the study area probably is not conducive to fungal growth. Moreover, river red gum decays much more slowly than timbers known to support rich saproxylic faunae (e.g. beech Fagus sylvatica, Douglas fir Pseudotsuga menziesii (Mirbel)) (Thorton et al. 1991; Bekele et al. 1997). The decay resistance of river red gum probably is due to high concentrations of biocidal phenols in the wood (Conde et al. 1995; Bekele et al. 1997; sensu Kelsey and Harmon 1989).

The habitat 'value' of logs on floodplains is a composite of the contribution to biodiversity during the dry phase and the wet phase. The faunal assemblage using logs as habitat during flooding was very different to the terrestrial fauna. However, the diversity of aquatic taxa on river red gum logs immersed in floodwaters also was low, with a mean of 3.6 ± 0.7 species per log 6 wk after inundation commenced. In flowing streams, after colonization for 8 wk, O'Connor (1991) recorded species richness of invertebrates on similar-sized river red gum logs an order of magnitude greater than in the current study. In the current study, the floodwater covering the logs was fairly stagnant and dark brown, indicating high levels of phenolic compounds. Gehrke (1993) demonstrated that river red gum leachates are toxic to juvenile fish. High concentrations of dissolved phenolics and low oxygen levels in the floodwaters probably restricted the number of invertebrate taxa able to colonize the submerged logs. Therefore, the low diversity of the log fauna during both the wet and dry phase probably is a result of the combined effects of environmental conditions and the chemistry of river red gum.

Scholz and Boon (1993) recorded high summer algal and bacterial abundance on river red gum timber submerged in a billabong and contended that biofilms on river red gum provide an important food source for grazing invertebrates. The capacity of larval chironomids to cope with poor water quality, together with their rapid life cycle, enabled the Kiefferulus species to numerically dominate the fauna on submerged logs. Maher and Carpenter (1984) also recorded high numbers of chironomids on sticks submerged in swamps and presented correlative evidence to suggest that flood-induced processes.

Thus, the strong patterns of association between fallen timber and obligate saproxylic invertebrates characteristic of relatively stable forest habitats were not seen in river red gum floodplain forest. However, river red gum logs appear to provide an important substrate for both terrestrial and aquatic invertebrates.

Faunal changes associated with structural complexity and flood disturbance

As river red gum logs age, they develop an increasing number of cracks and hollows partially as a result of the activities of invertebrates, such as termites. The 'honeycombing' process increases the structural intricacy of the log habitat. Hence, logs in more advanced stages of decay with many hollows supported a more abundant and diverse fauna than logs with few hollows. Working on smaller pieces of wood, Braccia and Batzer (2000) found invertebrate species richness, but not density, to increase with decay class. O'Connor (1991) contended that increased habitat heterogeneity and hence, the provision of a greater variety of resources, was responsible for increased species evenness on spatially-complex logs in streams, compared to logs with smooth surfaces. In the current study, it was not possible to use the same test as O'Connor (1991). The depauperate fauna and highly-clumped distributions of social insects made interpretation of any analysis of assemblage structure difficult. However, the composition of terrestrial-invertebrate assemblages in logs was not related to level of decay, suggesting that the variety of resources provided by logs may not change as the 'honey-combing' becomes more extensive.

The fauna in logs that had not been inundated for 1-2 yr was not significantly different in composition from that of logs immersed only 4 wk earlier. A nest of Iridomyrmex species (*mattiroloi* group) was recovered, with many queen pupae, from a log after 4 wk emersion. However, only five species were recovered from logs at 4 wk emersion, so that faunal similarities to unflooded logs were driven by very few species. The rapidity

chironomid abundance is important to waterfowl breeding. Therefore, despite being species poor, the aquatic fauna on river red gum logs may contribute to ecosystem

of the recolonization process is indicative of a high level of faunal resilience to flooding. Because no terrestrial taxa were found in the logs during flooding, it can be inferred that the terrestrial fauna successfully found refugia from floodwaters in habitat other than logs (see Chapter Six). Décamps (1993) contended that riparian biota only can achieve a quasi-equilibrial state when the interval between flood-disturbance recurrence is sufficient to allow recovery. My results suggest that the recovery time is so rapid that the quasi-equilibrial is stable in the face of variable flood patterns.

In contrast, the composition, but not the species richness, of invertebrate assemblages differed between logs that had been submerged one year earlier and logs that had not been inundated for many years. Thus, when flood frequency is reduced by river regulation, the fauna is likely to undergo a compositional shift, probably to less flood-tolerant species. To conclusively establish whether the fauna in dry areas is unable to cope with flooding, an experiment needs to be performed whereby logs are transferred from dry areas to flood-prone areas and the response of the log-dwelling fauna to inundation is assessed.

The response of abundance and species richness of log-dwelling invertebrates to flooding varied with the structural complexity of the log (Table 2.2). The abundance of invertebrates was reduced most by flooding in logs in the two most advanced decay classes. Species richness was greater in logs with extensive hollows (decay class 4) from dry areas compared to flood-prone areas. In contrast, species richness was similar, but very low, between logs with few hollows from dry areas and flood-prone areas. This suggests that the relationship between habitat structure and biodiversity varies according to the frequency of flood perturbation. However, species richness was similar in logs with very extensive hollows (decay class 5) between flood-prone and dry areas. This may reflect a switch from increasing habitat complexity to decreasing habitat complexity in the final stages of log decay, when much of the wood has been lost and the log is essentially a hollow shell.

Thinking in floodplain ecology has emphasized the primacy of flood perturbation as a mechanism for generating heterogeneity. Variability in inundation patterns is considered necessary to maintain floodplains as mosaics of habitat at different successional stages, sustaining high beta diversity (Ward and Tockner 2001). There has

been little recognition of the interaction between large-scale flood process and finegrain habitat structure (but see Odum 1990). Trebino *et al.* (1996) examined the interaction of successional stage and flood duration on species richness of plants in abandoned, agricultural land. They found that flood stress reduced diversity and that species richness was greatest at early successional stages. In contrast, my results suggest that while flooding influences the composition of the fauna at larger spatiotemporal scales, habitat structure is the primary determinant of diversity at small scales for mobile species. The spatial variability in habitats created by having logs in various stages of decay, together with the temporal habitat variability created by floods, contribute to maintaining invertebrate biodiversity in river red gum logs, despite the absence of a highly specialized saproxylic fauna.

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Table 2.1. Characteristics 1 1999).

Decay class	Log charac
0	Solid log re
1	Sound timb
2	A few holl
	limited rot
3	Moderate h
4	Extensive h
5	Very extens
	wood fragm

Table 2.1. Characteristics used to assign logs to decay classes (after Lindenmayer et al.

eristics
ently fallen, no rot, bark intact
r with minimal hollows and/or rot, no bark
ws often between the sapwood and the heartwood; may be
llows; may be moderate rot and some cracks in the wood
llows; may also be extensive rot and cracks in the wood
ive hollows; log essentially a shell packed with decomposed

nents; may also be very extensive rot

Variable	Model terms Decay class	Flood status	Interaction	Residual
Individiduals ^a /log				
d.f.	5	1	5	56
MS	13.58	1.28	12.00	4. 84
F	2.81*	0.27	2.48*	_
Richness/log				
d.f.	5	1	5	56 [°]
MS	19.73	0.03	10.86	3.39
F	5.83**	0.01	3.21*	-
^a Data log-transform	ned	<u> </u>	· · · · · · · · · · · · · · · · · · ·	· <u>·····························</u>

Table 2.2. Results of two-factor analysis of variance for (1) abundance and; (2) species richness of invertebrates in destructively sampled logs 2001.

*P < 0.05

** P < 0.005

Table 2.3. Two-way crossed analysis of similarities (R-statistics) for destructive sampling of logs in 2001 (data square-root transformed).

	Factor	
<u></u>	Decay class	Flood status
Global R	0.03	0.25**
Pairwise R Brief/no flooding vs. moderate flooding Brief/no flooding vs. extended flooding Moderate flooding vs. extended flooding	0.03 0.03 -0.04	

***P* < 0.005

Morphospecies	Av. abundance unflooded logs	Av. abundance flooded logs	Similarity/standard deviation	% Dissimilarity contribution
Coptotermes acinaciformis (Froggatt)	745.1	3.0	0.62	19.3%
(Isoptera: Rhinotermitidae)				
Doleromyrma sp. (darwiniana gp)	208.7	0.1	0.56	15.1%
(Hymenoptera: Formicidae)				
Iridomyrmex sp. (mattiroloi gp)	0.1	58.6	0.43	9.0%
(Hymenoptera: Formicidae)				
Monomorium sp. (laeve gp) (Hymenoptera: Formicidae)	4.7	23.4	0.34	7.3%
<i>Grymeus yanga</i> Harvey (Araneae: Oonopidae)	0.9	0.1	0.53	6.7%
Fhysanura sp. (Thysanura: Lepismatidae)	0	1.0	0.50	5.7%

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Table 2.5.	Results	of one-factor	(stage in	flood	cycle)	analysis	of	variance	for (1	i)
abundance	and; (2)	species richnes	s of inver	tebrate	s in des	tructively	san	npled log	s 2002	<u>!</u>

Variable	Model terms	
	Stage in flood	Residual
	cycle	
Individiduals ^a /log		
d.f.	4	23
MS	18.55	3.61
F	5.14**	_
Richness/log		
d.f.	4	23
MS	9.04	1.91
F	4.74*	
^a Data log-transform	ned	

*P < 0.05

** *P* < 0.005

Table 2.6. Results of paithe flood cycle.

Pairwise comparison

2wk inundated and 6wk inu 2wk inundated and 1wk em 2wk inundated and 1wk em 2wk inundated and 2001 2wk inundated and 2002 un 6wk inundated and 1wk em 6wk inundated and 4wk em 6wk inundated and 2001 6wk inundated and 2001 6wk inundated and 2002 un 1wk emersed and 2002 un 1wk emersed and 2002 un 4wk emersed and 2001 4wk emersed and 2001

	Possible	R	P
	permutations		
undated	126	0.656	0.008
nersed	35	0.750	0.029
nersed	35	0.667	0.029
	10626	0.484	0
nflooded	126	0.253	0.056
nersed	126	0.928	0.008
nersed	126	0.875	0.008
	53130	0.525	0
nflooded	126	0.600	0.008
ersed	35	0.589	0.029
	10626	0.439	0.002
flooded	126	0.438	0.024
	10626	0.067	0.616
flooded	126	0.050	0.349
	53130	0.130	0.150

Table 2.6. Results of pairwise analysis of similarities of log fauna at different stages in



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Figure 2.1. Photograph. of logs anchored against movement during flooding.

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(b) mean (\pm SE) invertebrate species richness per log for logs in different decay classes.

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Figure 2.3. (a) Mean (\pm SE) invertebrate abundance per log at different stages of the flood cycle; (b) mean (\pm SE) invertebrate species richness. per log at different stages of the flood cycle. Different letters correspond to significantly different values (P < 0.05).



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Figure 2.4. Non-metric multidimensional scaling plot of log fauna at various stages of inundation and emersion.) (stress = 0.04). (Arrows link consecutive sampling times.)

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			Pseudoscorpionidae
			sp.2
			Pseudoscorpionidae
			sp.3
:	Scolopendria		Scolopendria sp.1
(Geophilida		Geophilida sp.1
:	Scutigerida		Scutigerida sp.1
]	Isopoda		Isopoda sp. l
	Thysanura	Lepismatidae	Lepismatidae sp. l
	lsoptera	Rhinotermitidae	Coptotermes
			acinaciformis
			(Froggatt)
ı	Coleoptera		
		Curculionidae	Talaurinus howittii
		(Amycterinae)	Macleay
		Curculionidae	Curculionidae sp.1
		Pselaphidae	Articerus sp.1
			(?)Hamotopsis sp.1
		Dermestidae	Orphinus sp.1
		Anthicidae	Anthicus sp.1
		Lathridiidae	Corticaria sp.1
		Staphylinidae	(?)Tachinus sp.1
		(Tachyporinae)	

Order	Family	Genus
		(?)Tachinus sp.2
	Staphylinidae	Staphylinidae sp.
	(Aleocharinae)	

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Tenebrionidae

Carabidae

(Harpalinae)

(Bembidiinae)

Carabidae

Formicidae

Hymenoptera

Coleoptera sp.1 Chalcopteroides sp.1 Egadroma (?)vestigialis Erichson

Bembidion sp.1

Paratrechina

(obscura gp) Rhytidoponera

Iridomyrmex

Stigmacros

(intacta gp)

Monomorium

D)

gp)

Pheidole sp. 1 (Group

Ochetellus sp. 1 (glaber

(mattiroloi gp)

metallica (Smith)

sp.1

sp.1

sp.1

sp.1

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Appendix 2.1 continued

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Ref. Class

sp.1(laeve gp) Crematogaster (laeviceps gp)

Doleromyrma sp.1 (darwiniana gp) Iridomyrmex sp.4 Bothriomyrmex sp.1

CHAPTER THREE

PROVISION OF HABITAT FOR INVERTEBRATES BY FALLEN TIMBER AT TWO SPATIAL SCALES IN RIVER RED GUM EUCALYPTUS CAMALDULENSIS FLOODPLAIN FOREST

Abstract

Fallen timber may affect forest-floor <u>stabilestic</u> y enhancing structural. nplexity and by providing a nesting substrate for ground-foraging invertebrates. The impact of fallen timber on the surrounding fc.est-floor invertebrate assemblages was investigated in river red gum *Eucalyptus camaldulensis* floodplain forest at two spatial scales: (1) within a 5 m zone around logs; and (2) at 0.25 ha sites with varying volumes of fallen timber. At the 5-m scale, the abundance and species richness of taxa generally increased with proximity to logs. The composition of forest-floor invertebrate assemblages also sometimes varied with distance from fallen timber. Coverage of leaf litter was shown to be greatest adjacent to logs and, thus, variation in the leaf-litter microhabitat might account for the small-scale differences in invertebrate assemblages.

To measure the 'mean' effect of fallen-timber load at the 0.25-ha scale, traps were positioned randomly within sites with known fallen-timber loads. Little evidence was found for changes in abundance or species richness of taxa with increasing fallen-timber load. However, the composition of assemblages sometimes was related to fallen-timber loads. Fallen-timber load might be correlated with the probability of a random sample being taken close to a log and hence, the sample contents being influenced by smallscale processes mediated by that log. To investigate the 0.25-ha scale effect of fallentimber load independently of proximity to fallen timber, traps were positioned adjacent to logs at sites with a range of fallen-timber loads. No relationship was found between fallen-timber load and any characteristic of invertebrate assemblages. Therefore, the strongest effects of fallen timber on invertebrate assemblages occur at small scales.

Introduction

Graham (1925) first identified logs as "ecological units" with a distinct fauna. In the last two decades, research directed at improving forestry management practices has explored extensively the role of logs as habitat. An array of taxa has been shown to use fallen timber (coarse woody debris) as habitat, including: plants, fungi, small mammals, birds and many terrestrial invertebrates (Harmon *et al.* 1986; Stevens 1997; Butts and McComb 2000; Mac Nally *et al.* 2001; Lohr *et al.* 2002). For invertebrates, logs provide food, shelter from extreme environmental conditions and oviposition sites (Harmon *et al.* 1986).

River red gum *Eucalyptus camaldulensis* Denhn. forests occur on the floodplains of rivers in south-eastern Australia. Identifying how fallen timber functions as habitat is a management issue in river red gum forests because large volumes of fallen timber have been removed from these forests as a result of human activities (Mac Nally and Parkinson 1999). This habitat simplification has been shown to negatively affect native vertebrates (Mac Nally *et al.* 2001). The effects of removal of fallen timber on invertebrates are uncertain because the role of river red gum logs as habitat for invertebrates has not been investigated widely.

In Chapter Two, river red gum logs were shown to provide habitat largely for generalist species, particularly ants, that are thought to forage on the forest floor, rather than remaining inside a single log. The termite *Coptotermes acinaciformis* (Froggatt) is an exception because it excavates subterrancan tunnels to reach food sources (Hadlington 1987). An ant nest in a log represents a centre of foraging activity that could affect invertebrate assemblages on the surrounding forest floor, creating a 'halo' of influence around the log. Moreover, Lowrie (1948) and Lloyd (1963) described movement of spiders and other invertebrates between logs and adjacent leaf litter in response to diurnal and climatic cues. Thus, Graham's (1925) view of logs as discrete, isolated "ecological units" is unlikely to be applicable in river red gum forest. The effect of logs on the surrounding forest-floor habitat needs to be considered to develop a more comprehensive understanding of the ecological function of fallen timber.

The presence of a log may have small-scale effects, altering the forest-floor microhabitat immediately surrounding the timber by changing nutrient retention rates and moderating humidity and temperature (Harmon *et al.* 1986). In addition, the load of fallen timber may influence the habitat characteristics of the forest floor at larger scales. For instance, Schiegg (2000) demonstrated that the degree of connectivity of fallen timber influenced the species richness and composition of saproxylic (dead-wood associated) insects at the 150-m scale.

Recent studies of the habit associations of small vertebrates have investigated the effects of fallen-timber loads across multiple scales (Bowman et al. 2000; Butts and McComb 2000). Reseachers generally have assessed the effect of fallen timber at scales of 10s to 100s m by sampling randomly, or in a grid, and correlating characteristics of faunal samples with fallen-timber loads. As the amount of fallen timber on a given area increases, the proximity of random points to fallen timber also may increase. The higher the fallen-timber load, the more likely a sample is to have been taken at a point close to a log and, therefore, to be affected by small-scale, local habitat change associated with the presence of that log. Thus, this method of sampling assesses the 'mean' effect of many logs, each creating localized habitat change (Fig. 3.1). However, this method does not test for the any overarching influence of fallen timber at the site scale that might act independently of proximity to timber. For instance, as fallen-timber load increases across a range of sites, populations of a hypothetical, mobile insectivore also might increase. This insectivore causes a uniform reduction in invertebrate populations at each site to a density inversely correlated with the site fallen-timber load. Within each site, invertebrate densities are maximal adjacent to logs regardless of fallen-timber load. Random sampling would not detect the effect of the insectivore because samples collected from sites with lower fallen-timber loads would be more likely to be taken at points further away from logs and, therefore, to contain fewer invertebrates (Fig. 3.1).

Failing to distinguish between larger-scale processes and an increase in small-scale (per log) processes caused by greater fallen-timber loads could result in the underestimation of the habitat value (per log) of fallen timber at low densities. Correlation between fallen-timber load and the probability of a random point being close to a log is reduced

when fallen timber has a highly clumped distribution. Similarly, for highly mobile organisms, smaller-scale processes are likely to be subsumed by larger-scale processes.

In the present study, I examine the effects of fallen timber on forest-floor invertebrates at the scale of 5 m and 0.25 ha. Invertebrates were sampled intensively in a 5-m zone around fallen timber to determine if logs act as 'hotspots' of terrestrial invertebrate activity. The invertebrate fauna in 0.25 ha sites, with known fallen-timber loads, was sampled with randomly positioned traps to determine whether patterns observed at the 5-m scale hold at larger spatial scales. I tested for correlation between site fallen-timber load and proximity of randomly placed traps to logs. Last, to assess 'larger-scale' effects of site fallen-timber load, I took samples in identical positions relative to logs at sites with a range of fallen-timber loads. By taking samples in the same position relative to the nearest log, I hoped to control for variability caused by small-scale processes.

Methods

Study area

This work was conducted in Barmah State Forest and Barmah State Park in northern Victoria, Australia, about 215 km from Melbourne (35°55'S 145°08'E). Barmah Forest occurs on the Murray-River floodplain where the channel has unusually low capacity. The Murray River and many anastomosing creeks run through the forest. Soils are stratified layers of clay overlaid by sand (Silvers 1993). Barmah Forest consists largely of monospecific stands of Eucalyptus camaldulensis with an understorey of grasses, rushes and sedges (Chesterfield 1986). The forest experienced extensive flooding in the austral spring 2000, with floodwaters receding in early summer 2001.

Sampling Protocol

Invertebrate activity—5 m around logs

To examine the response of ground-active invertebrates to the presence of fallen timber in the immediate vicinity, pitfall traps were placed in a grid formation on one side of large (1 m diameter) fallen logs. Grids consisted of six rows of four traps spaced at 1 m intervals between 0 m and 5 m from the log, giving 24 traps per log. The contents of the four traps in each row were considered to be sub-samples and were pooled. Pitfall trapping of logs was conducted in January 2001 (five logs), May 2001 (four logs), November 2002 (four logs) and January 2003 (four logs). Preliminary results suggested that species that use leaf litter as habitat largely were responsible for trends in the data. Consequently, leaf-litter cover was measured in November 2002 and January 2003. To measure the extent of litter accumulation against logs, a 0.10 m \times 0.10 m wire quadrant was placed over the ground where each pitfall trap was to be located and percentage cover of leaf litter then was estimated.

Invertebrate activity-0.25 ha sites

Sixteen 0.25 ha study sites were chosen to have a range of fallen-timber loads, eight of the sites were selected to have high fallen-timber loads (> 50 t ha⁻¹) and eight to have low fallen-timber loads (< 20 t ha⁻¹). Five pitfall traps were used to sample invertebrates at each study site and the contents of the traps were pooled into a single sample. Pitfall traps were spaced 2 m apart, in a randomly positioned line, for ease of re-location. The position of the trap line within the study site was changed at every sampling time. Sites were surveyed nine times during the study: May 2000, August 2000, January 2001, May 2001, August 2001, November 2001, January 2002, November 2002 and January 2003. Widespread flooding prevented sampling in November 2000. Due to cold weather, the catches of spiders and beetles during the August sampling periods were deemed to be too small for statistical analysis and consequently, have been excluded. In November 2001 and January 2002, the distances between 80 of the randomly placed pitfall traps and the nearest piece of fallen timber were measured at the eight high fallen-timber sites. (Data from two sites were lost.)

To assess 'larger-scale' effects of fallen timber on forest floor invertebrates, independent of proximity to logs, eight more 0.25 ha sites with a range of fallen-timber loads were selected in January 2001. Each site was sampled with five pitfall traps. Every pitfall trap was positioned adjacent to a separate log and the sampled logs were spaced ca 2 m apart. The eight additional sites were surveyed concurrently with the other 16 sites, excluding the May 2000 and August 2000 surveys.

The load of fallen timber was assessed at each site by using a tape to measure the length and end diameters of every piece of wood of diameter ≥ 0.10 m on each study site. Fallen-timber loads were assumed to be constant at each site throughout the study period. This assumption is reasonable given the slow rate of decay of river red gum logs. However, small changes in fallen-timber loads did occur through the study due to tree fall and firewood harvesting. A large tree fell at one of the low fallen-timber sites, increasing fallen timber at that site to 26.9 t ha⁻¹ at the time that fallen-timber loads were surveyed, but data from that site still were included in the analysis.

The study area is a floodplain and the extent of local flooding is an important factor influencing invertebrate faunae at the 0.25 ha site scale (see Chapters Two, Four and Five). Consequently, sites were categorized by the duration of inundated experienced in the major flood, immediately before sampling in January 2001 (brief/no inundation, moderate inundation, extended inundation). In November 2002, three sites were inundated a second time and in December 2002, one additional site was inundated. Data collected from sites after a second inundation were excluded from the analysis.

Pitfall trapping and sample-processing protocol

Pitfall traps with an opening diameter of 75 mm and a depth of 95 mm were used for all trapping. Traps were closed for ≥ 24 h following installation to counter possible 'digging-in' disturbance effects (Greenslade 1973) (see below). Pitfall traps then were filled with a 70% propanol: 5% glycerol: 25% water solution and opened for five days and nights.

On being returned to the laboratory, trap contents were sieved to 1 mm² and specimens were stored is a 70% ethanol: 30% distilled water preservative. Samples were sorted to morphospecies and adult ant, beetle and spider specimens were identified to the highest practicable taxonomic level. Expert taxonomic assistance was sought (see acknowledgements).

Critique of invertebrate survey techniques

Pitfall trapping was used for much of the sampling in this project (Chapters Four, Five and Six). This method is cheap and easy (Southwood 1966), avoids problems of spot sampling in time and can result in large catches (Topping and Sunderland 1992). However, like all survey methods, pitfall trapping introduces biases into the data, which influence the conclusions drawn. The likelihood of an individual being caught in a pitfall trap depends on its activity level. Activity levels vary between species and sexes due to differential mate-searching efforts, food-searching efforts, as well as postcopulatory dispersal of females (see Merrett 1967; Topping and Sunderland 1992). The size (Abensperg-Traun and Dion 1995; Brennan *et al.* 1999; Work *et al.* 2002) and layout (Ward *et al.* 2001) of pitfall traps also can influence the abundance, species richness and/or composition of the catch.

The extent of trapping bias differs between taxonomic groups. Curtis (1980) found broad agreement between pitfall trapping and other survey methods for the relative abundance and species richness of spiders, although single species may show inconsistent relationships between density and catch-rates through time (Curtis 1980; Topping and Sunderland 1992). Pitfall trapping has been advocated as a reliable measure of the relative size of carabid beetle populations (Baars 1979), although trapping bias in the ratio of males to females has been documented in species that exhibit parental care (Home 1990). The use of alcohol in the preservative solution may attract disproportionately large numbers of beetles associated with decaying organic material (Greenslade and Greenslade 1971). Greenslade and Greenslade (1971) recommended pitfall traps as a survey method for ants, noting that ants do not appear to be attracted to an alcohol: glycerol: water preservative solution. Majer (1997) and Melbourne (1999) recorded bias in ant pitfall catches, particularly in species composition, when the ground layer is complex. In the present study, ground cover, including the litter layer, never appeared to be very deep or dense.

Greenslade (1973) documented a 'digging-in' effect for ants whereby catches in pitfall traps were initially high and subsequently declined. The main reason for the effect is thought to be that ants investigate the soil disturbance created when a pitfall trap is dug into the ground and so, initially are attracted to the trap. Greenslade and Greenslade (1971) recommended leaving pitfall traps in the ground for a week before opening them. This recommendation is derived from a study where traps were cleared at 2-4 d intervals and, as a result, it is not known if a shorter 'resting' period would suffice to eliminate 'digging-in' effects.

Many of the sources of bias described above do not create major problems for the current project because the same trapping procedure was used at all times. Moreover, faunal comparisons between sites mostly are restricted to one survey period, when trapping bias is assumed to be constant across all sites. Some authors substitute the

cumbrous term "activity-density" for abundance, in recognition of the influence of activity levels on pitfall capture rates. Here, I use the term "abundance," but I acknowledge that the relationship between capture rates and actual densities is not necessarily straightforward.

Analyses

Justification of statistical methods used

Many of the data analyses in this thesis are performed using frequentist statistical methods, which are widely used and, therefore, familiar to readers. However, frequentist statistical methods were not adequate for some of the analyses required. The study was a repeated-measures design, with up to nine visits to the same study sites. Three sites and four sites had to be excluded from the November 2002 and January 2003 analyses respectively because there were second floodings. Conventional repeated-measures ANOVA designs do not cope well with missing data, particularly when the data are missing in a fairly systematic fashion, as was the case in this chapter (Quinn and Keough 2002). Here, data for flood-prone sites were more likely to be unavailable from the last two sampling periods. Using a Bayesian approach to some data analysis was considered preferable to jettisoning one sixth of the data. While there are philosophical problems with using a combination of frequentist and Bayesian analyses (cf. Quinn and Keough 2002), from a utilitarian perspective, this was deemed to be the best compromise to deal with a complex, incomplete sampling design.

Statistical software used

Analyses of variance (ANOVA) were performed with SYSTAT (Version 10, SPSS Inc. 2000). Analyses of similarities (ANOSIM), similarity percentage analyses (SIMPER) and Mantel tests (RELATE) were conducted with PRIMER (Version 5, Clarke and Gorley 2001). The Bayesian analyses were implemented by using WinBUGs (Version 1.4, Spiegelhalter et al. 2003), which uses the Metropolis-Hasting algorithm with Gibbs parameters.

Invertebrate activity-5 m around logs

The analyses performed on the pitfall-trap data were repeated-measures ANOVAs with one between-factor (season) and one within-factor (distance from log). The dependent variables were the abundance or the species richness of total taxa (spiders, beetles and ants summed together), as well as spiders, beetles and ants considered separately.

To examine changes in invertebrate-assemblage structure 5 m around logs, Bray-Curtis similarity matrices were computed for the pitfall-trap data. Pitfall-trap data were square-root transformed to reduce the influence of very abundant species on the analyses. The pitfall-trap data were re-categorized into two groups (≤ 1 m from log, ≥ 4 m from log), and data from the intermediate distances (2-3 m) were excluded from the analyses to increase the contrast between the proximate and distant groups, before onefactor ANOSIMs were performed with proximity to log as the contrasting factor. ANOSIMs were conducted separately for each sampling period and for each taxon (spiders, beetles, ants). Due to the numerical dominance of ants, an ANOSIM was not conducted on the pooled results for all taxa (i.e. spiders, beetles and ants). SIMPER analyses were performed on the data to identify species contributing most to differences between assemblages ≤ 1 m from logs and ≥ 4 m from logs. The ratio of the mean to the standard deviation of the dissimilarity values was calculated for each influential species as a measure of the consistency of the distribution/habitat affiliation patterns of the species considered. This measure, essentially the inverse of the coefficient of variation, is calculated within PRIMER. Clarke and Gorley (2001) contended that a dissimilarity mean/standard deviation ratio ≥ 1.4 indicates high habitat fidelity.

The mean percentage of leaf-litter cover was calculated for the four sub-samples taken at each distance from logs. A repeated-measures ANOVA was performed on mean percentage leaf-litter cover with one between-factor (sample time: November 2002, January 2003) and one within-factor (distance from log: 0-5 m).

sampling to construct the joint posterior probability distributions of the model

Invertebrate activity -0.25 ha sites

To calculate fallen-timber loads, each log was assumed to be a truncated cone of volume (V) (m³) such that:

$$V = \pi L (r_1^2 + r_1 r_2 + r_2^2)/3$$

where L is the length of the log (m) and r_1 and r_2 are the radii of the two ends (m) (Harmon and Sexton 1996). Logs were assumed to have uniform density of 0.6 t m⁻³ (Robinson 1997). The volumes of all logs on the site were summed and transformed into t ha⁻¹. A Pearson correlation then was calculated between fallen-timber load and the mean distance of randomly placed pitfall traps from logs, at the six sites for which data were available.

To analyze the effect of fallen-timber load and flood duration on the abundance of taxa the same model was run separately for the 16 sites with randomly positioned traps and the eight sites with traps positioned adjacent to fallen timber. I used this Bayesian model:

$Y_{i(i)k} \sim \text{Normal}\left(\mu_{i(k)}\sigma_{ik}\right)$ $\mu_{j(i)k(l)} = \alpha_l \lambda_{k(l)} + \beta_i \pi_{j(l)} + \gamma \phi_j + \sigma_j + \sigma_{jk}$

Y is the natural logarithm of (number of spiders/beetles/ants) caught at study site i at sample time k. Y is distributed normally with mean μ and standard deviation σ . The duration of inundation at study site *j* in spring/summer 2000-2001 is indicated by the subscript *i*. Whether the survey was conducted in a spring/summer or autumn/winter is denoted by l. α models the effect of sampling in the cooler seasons (autumn or winter) on Y, and λ are elements of a matrix that identifies each survey as being conducted in autumn/winter (May, August) ($\lambda = 1$) or spring/summer (November, January) ($\lambda = 0$). β s model the effect of duration of local flooding in spring/summer 2000–2001 on Y and π are elements of a matrix that identify each site as belonging to a particular flood treatment (brief, moderate or extended inundation). γ accounts for the effect of deviation from mean fallen-timber load (ϕ) at each site on Y. The σ_i are site random effects, while the σ_{ik} are site-repeated-survey random effects (Breslow and Clayton 1993). Non-informative, normally distributed priors where used to seed the model.

A variation on the model was used to examine the effect of fallen-timber load and local flood duration on the species richness of each taxonomic group for both the 16 . *es with randomly positioned traps and the eight sites with traps adjacent to logs. Given that species richness is expected to be a Poisson-distributed variable (i.e. consisting of small, non-negative integers), it was necessary to include a link function in the model, such that:

In the current study, I adopted the simple decision-making criterion of Mac Nally and Horrocks (2002) for identifying 'important' factors. Bayesian analysis provides a posterior probability distribution for each of the model parameters (and combinations thereof, such as the difference between any two parameters). The proportion of the posterior probability distribution lying above zero is referred to as the posterior probability mass (PPM). When a model parameter has no effect on the dependent variable, the posterior probability distribution is centred on zero and the expected value of PPM is 0.50. Model parameters with \geq 90% of the posterior probability distribution lying above zero (i.e. PPM ≥ 0.90) were considered to have a 'substantial' positive • effect on the dependent variable. For parameters with a negative coefficient, \geq 90% of the posterior probability distribution lies below zero to be classed as 'substantial,' giving a PPM ≤ 0.10 .

Mantel tests were used to compare similarities in faunal assemblages between sites with similarities in fallen-timber loads, using an untransformed Bray-Curtis matrix of similarities in site fallen-timber loads and the similarity matrices already generated for each taxon. Separate tests using a maximum of 20 000 randomizations were conducted for spiders, beetles and ants at each sampling period.

$$Y_{j(i)k} \sim \text{Poisson} (\mu_{jk})$$
$$\ln(\mu_{j(i)k(l)}) = \alpha_l \lambda_{k(l)} + \beta_l \pi_{j(l)} + \gamma \phi_l + \sigma_l + \sigma_{jk}$$

The model parameters are as described above for the abundance model.

Results

Invertebrate activity-5 m around logs

Patterns of species richness and abundance differed between sampling times, so the results are depicted separately for each taxon at each sampling time (Table 3.1, Fig. 3.2a- d). Total abundance of the three taxa (spiders, beetles, ants) pooled, as well as the abundance of spiders and ants separately, varied across a 5 m zone around logs, generally declining at greater distances from fallen timber (Table 3.1, Fig. 3.2a-d). However, in some cases the minima occurred at an intermediate distance from logs (Table 3.1, Fig. 3.2a-d). Beetle abundance did not vary with log proximity (MS = 1.60, $F_5 = 2.32$, $P \approx 0.053$). The species richness of spiders, beetles and all taxa pooled declined with increasing distance from fallen timber (Table 3.1, Fig. 3.2a-c). No relationship was found between the species richness of ants and proximity to fallen timber (Table 3.1, Figure 3.1d).

Changes were found in the composition of assemblages at 0–1 m from logs compared to 4–5 m from logs in May 2001 and November 2002, but not during the two January sampling periods (Table 3.2). Different densities of two species of log-nesting ants, *Iridomyrmex* sp. (*mattiroloi* gp.) and *Paratrechina* sp. (*obscura* gp.) largely were responsible for differences in the composition of ant assemblages with varying proximity to logs in both May 2001 and November 2002 (Table 3.3). The beetle species influential in creating changes in beetle assemblages at different distances from logs changed between May 2001 and November 2002, reflecting seasonal activity patterns (Table 3.3). Several of the influential taxa are from families typically associated with leaf litter including: *Nargomorphus* sp. (Coleoptera: Leiodidae), *Brachypeplus* sp. (Coleoptera: Nitidulidae) and *Grymeus yanga* Harvey (Araneae: Oonopidae) (Table 3.3). The dissimilarity mean/standard deviation ratios were relatively low for species contributing most to dissimilarity between assemblages at 0–1 m and 4–5 m from logs, ranging from 0.61 to 1.67 (Table 3.3).

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The percentage of ground covered by leaf litter declined with increasing distance from fallen timber (Table 3.4, Fig. 3.3), suggesting that the resources available for leaf-litter dependent species are at a maximum immediately adjacent to fallen timber. No difference in leaf-litter cover was found between the November 2002 and January 2003 sampling periods, so seasonal changes in volume of leaf litter do not explain differences in assemblage responses to log proximity between the last two sampling times.

Invertebrate activity-0.25 ha sites

Fallen-timber loads at the 16 sites where pitfall traps were placed randomly ranged from i-118.9 t ha⁻¹. No correlation was found between the mean distance of randomly positioned traps from fallen timber and fallen-timber load at the six sites tested ($r = 0.689 P \approx 0.13$).

Whether a survey was conducted in autumn/winter or spring/summer, and the duration of local flooding in 2000–2001, had substantial effects on the fauna at the 0.25-ha sites (Tables 3.5–3.16). These factors are discussed in detail in Chapters Four and Five.

In general, there was no relationship between the abundance or species richness of taxa caught in randomly placed traps and the volume of fallen timber in the surrounding 0.25 ha (Table 3.5–3.10). However, fallen-timber load had a substantial negative effect on the abundance of beetles (Table 3.6).

Similarity of assemblage structure was correlated with similarity in fallen-timber loads between sites for spiders in January 2003 (R = 0.243, $P \approx 0.034$). The composition of beetle assemblages was related to site fallen-timber loads in January 2001(R = 0.273, $P \approx 0.001$) and November 2001 (R = 0.219, $P \approx 0.039$). Moreover, similarity in site fallen-timber loads was correlated with similarity in ant assemblages in January 2002 (R = 0.230, $P \approx 0.046$) and January 2003 (R = 0.312, $P \approx 0.007$). There was no evidence for an influence of fallen-timber load on other aspects of assemblage composition and, therefore, the results of the other Mantel tests are not reported here. There was no relationship between the abundance or species richness of taxa caught in traps positioned adjacent to logs and the fallen-timber load in the surround 0.25 ha (Table 3.11-3.16), despite fallen-timber loads ranging between 40.8-126.2 t ha⁻¹. Furthermore, when traps were positioned next to logs, similarity of invertebrate-assemblage structure and similarity of fallen-timber loads were uncorrelated. Consequently, the results of the Mantel tests are not reported here.

Discussion

Invertebrate activity-5m around logs

The structural complexity provided by logs promoted biodiversity at the scale of 5 m around logs. Proximity to fallen timber influenced abundance and species richness of all taxa pooled, as well as that of spiders (Table 3.1). Similarly, ant abundance depended on distance to logs, but no relationship was identified between the species richness of ants and proximity to fallen timber (Table 3.1). The highly patchy distribution and low diversity of ants on the floodplain might make it difficult to detect patterns. Andrew *et al.* (2000) found no relationship between the species richness of ants and proximity to relationship between the species richness of ants and proximity to logs in eucalypt forest in New South Wales that was not subject to flood disturbance.

Very few specialist saproxylic species were caught (see also Chapter Two). The majority of the beetles captured were detritivorous or fungivorous leaf-litter dwellers. This suggests that trapping leaf litter is the predominant mechanism by which logs promote biodiversity of forest-floor invertebrates. Leaf litter accumulated against logs is recognized as a spatially complex microhabitat for invertebrates (Uetz 1976; Andrew *et al.* 2000). In the current study, leaf-litter cover rapidly declined with increasing distance from logs (Table 3.4., Fig. 3.3). Litter depth has been shown elsewhere to influence the structure of spider assemblages (Bultman and Uetz 1982; Vargas 2000) and beetle assemblages (Koivula *et al.* 1999). Given that I did not experimentally manipulate litter levels, causality between higher invertebrate abundance and species richness closer to logs and greater leaf-litter cover was not demonstrated conclusively.

Bultman and Uetz (1982) and Lowrie (1948) suggested several reasons why increased litter depth may facilitate greater species richness of spiders. These included: more points for web-attachment, greater prey availability, and stratification and patchiness within litter layers. Lowrie (1948) and Lloyd (1963) described movement of spiders and other invertebrates between logs and adjacent litter habitat in response to diurnal and climatic cues. Although untested, the juxtaposition of log and leaf-litter habitat might, therefore, increase abundance and species richness of some taxa.

The litter-dwelling beetle *Nargomorphus* sp. was responsible for much of the variation in the structure of pitfall-trapped beetle assemblages between 0–1 m and 4–5 m from logs in May 2001 (Table 3.3). *Nargomorphus* sp. belongs to the Cholevinae, a subfamily containing species known to be sensitive to soil-moisture levels and variations in substrate temperature (Tizado and Salgado 2000). These factors vary across small spatial scales in relation to leaf-litter cover (e.g. Dighton *et al.* 2000). However, no consistent pattern was identified for *Nargomorphus* sp.; its contribution to group dissimilarity was a result of high variability in catch size.

River red gum logs also promote biodiversity by providing nesting sites for ants that forage on the forest floor. The ant species *Paratrechina* sp. (*obscura* gp.) and *Iridomyrmex* sp.(*mattiroloi* gp.) were influential in generating dissimilarity in ant assemblages with distance from fallen timber in both May 2001 and November 2002. The nests of these ant species commonly were encountered during destructive sampling of logs, with four and eleven nests of the *Paratrechina* sp. and the *Iridomyrmex* sp. respectively excavated from 68 logs in 2001 (Chapter Two). Therefore, the decrease in abundance of those species with increasing distance from the log probably reflects a radial spatial distribution of activity around the nest. Increased activity of ants around fallen timber was not associated with a decline in potential prey species, such as beetles, suggesting that abiotic factors, rather than biotic interactions, are paramount in determining small-scale invertebrate distribution patterns.

Invertebrate activity-0.25 ha sites

Fallen-timber loads on 0.25 ha sites were not related to the abundance or species richness of invertebrates sampled with randomly placed pitfall traps. Beetle abundance was the exception, declining with increasing fallen-timber load at 0.25-ha (Table 3.6), despite being insensitive to distance from logs at the 5-m scale. The apparent lack of a relationship at the 0.25-ha scale is not evidence that fallen timber is unimportant to forest-floor invertebrates. Variability created by randomly positioning traps might have obscured smaller-scale relationships between proximity to fallen timber and invertebrate biodiversity, such as were revealed at the 5-m scale.

The composition of invertebrate assemblages sometimes was related to fallen-timber loads. This may be a result of the 'mean' effect of small-scale processes mediated by single logs increasing as fallen-timber load increased. However, the correlation between fallen-timber load and the mean distance from randomly placed traps to fallen timber was not important. This partially was a result of low statistical power; only six sites, all with high fallen-timber loads, could be included in the correlation analysis.

To examine 'larger-scale' processes, independent of the effect of proximity to the nearest log, traps were placed adjacent to logs on sites with a range of fallen-timber loads. No relationships between site fallen-timber load and the abundance, species richness or assemblage composition of invertebrates were found, despite sites being sampled with fallen-timber loads ranging from 40.8–126.2 t ha⁻¹. This suggests that the fallen timber only affects forest-floor invertebrates at small spatial scales by processes mediated by individual logs.

Even in a comparatively generalized and vagile fauna, differences in insolation and leaflitter cover associated with fallen-timber loads were expected to influence forest-floor fauna at the site scale. Mac Nally and Horrocks (2002) observed that the insectivorous marsupial *Antechinus flavipes* increased in abundance in river red gum forest only when a threshold load of 40 t ha⁻¹ of fallen-timber was exceeded. This suggests that animals do not experience the habitat changes wrought by fallen timber in a linear fashion, at the 0.25-ha scale. Unfortunately, in the present study, none of the eight sites had a fallentimber load below 40 t ha⁻¹ and consequently, all sites might have been over a threshold \therefore where site-scale processes become insensitive to fallen-timber load.

This study design was limited in its capacity to critically examine effects of fallen timber across different spatial scales in two respects. First, at the 5-m scale, the use of a repeated-measures design controlled for the effect of subject (log), but no control for inter-log variability was possible at the 0.25-ha scale. Variability in fauna between logs might be a key factor explaining why results differed between the two spatial scales. Second, the study design did not take into account other structural components of study sites that might override effects of fallen-timber loads. In particular, the relationship between fallen-timber loads and leaf-litter levels was not established at the 0.25 ha site scale. Factors such as the availability of structures where leaf litter may accumulate (e.g. tree trunks, depressions in the ground) and the exposure of a site to winds will influence litter-retention rates.

Site-level factors that influence input and decay rates of leaf litter were not considered. Inundation promotes litter decomposition (Bell and Sipp. 1975; Ellis *et al.* 1999; Glazebrook and Robertson; O'Connell *et al.* 2000). However, in river red gum forests, flooding and post-flood drying also increase litter-recruitment rates (Briggs and Maher 1983; Stone and Bacon 1995). The highest activities of detritivorous beetles were recorded in autumn 2001, 4 mo after flooding (Chapter Four). Thus, understanding ecological processes across multiple scales is challenging not only because of the variable dynamics of natural systems, but also because there is often no straightforward method to measure the same variable across multiple scales.

The abundance and species richness of several invertebrate taxa varied with proximity to logs at the 5-m scale, suggesting that fallen timber influences biodiversity on the river red gum forest floor. This effect is likely to be mediated by leaf-litter accumulation against logs forming a spatially complex microhabitat and by radial activity-level patterns of log-nesting ants. At larger spatial scales, fallen timber appeared to have little discernible influence on invertebrate assemblages. However, the lack of clear patterns at the 0.25-ha scale does not demonstrate unambiguously that forest-floor invertebrates respond to heterogeneity created by fallen timber only at scales less than 0.25 ha because organisms may respond to fallen-timber loads at a given scale only within a

range of values. Therefore, structural components of the habitat mosaic play a role in maintaining biodiversity, even in a relatively generalized fauna, but 'scaling up' the effects of heterogeneity is difficult.

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(m). (a)

Factor	Abun	dance							
······		Total	a	Spide	rs ^b	Beetle	s ^b	Ants ^a	
	d.f.	MS	F	MS	F	MS	F	MS	F
Sampling time	3	41.64	21.62**	27.26	55.74 **	13.52	2.20	66.71	25.01"
Error	13	1.93	-	6.36	0.49	6.16	-	2.67	-
Distance to	5	0.72	4.32**	2.02	6.36**	1.60	2.32	1.13	3.74**
Distance to log × sampling time	15	0.28	1.67	0.43	1.36	1.33	1.93*	0.49	1.6]
Error	65	0.17		0.32		0.69	_	0.30	
^a data natural	log trans	sformed							
^b data square-	root tran	sformed							
** $P \le 0.005$									
$P \le 0.05$									

Table 3.1. Repeated-measures analysis of variance of (a) abundance; and (b) species richness of spiders, beetles, ants and all taxa against distance to the nearest fallen timber Table 3.1. continued

(b)

Factor		Specie	es Richne	SS					
		Total		Spide	rs	Beetle	es	Ants	
	d.f.	MS	F	MS	F	MS	F	MS	F
Sampling	3	693.1	27.45**	166.6	30.43	77.60	4.33 [*]	80.98	6.97 ^{**}
time Error	13	25.25	· -	5.47	-	17.93		11.62	-
Distance to	5	43.43	6.29**	8.06	2.92*	13.27	4.72**	0.42	0.26
log Distance to	15	12.35	1.79	3.58	1.30	4.21	1.50	1.00	0.62
log × sampling time									
Error	65	6.91		2.75	-	2.81		1.61	_

^a data natural log transformed

^b data square-root transformed

" $P \le 0.005$

 $P \le 0.05$

Table 3.2. Analysis of sim from logs.

Sampling event	Spiders ^a		Beetles ^a		Ants ^a	
····	Permutations	R	Permutations	R	Permutations	R
January 2001	20 000	0.03	20 000	-0.03	20 000	0.01
May 2001#	126	0.04	6435	0.18*	6435	0.15
November 2002	6435	0.15	6435	0.36**	6435	0.32**
January 2003	6435	0.09	6435	0.11	6435	-0.03

•• $P \le 0.005$ • $P \le 0.05$

Adult spiders were not permutations.

Table 3.2. Analysis of similarities between invertebrate assemblage 0-1 m and 4-5 m

Adult spiders were not recorded in all samples, reducing the number of possible

Table 3.3. Spider, beetle and ant species contributing most to dissimilarities between assemblages 0–1 m and 4–5 m from logs.

Sampling time	Taxa	Species	0-1 m av. abundance	4–5 m av. abundance	Dissimilarity/SD	% contribution to dissimilarity
May 2001	Beeties	Nargomorphus sp.	7.25	8.13	1.48	33.62
·		(Leiodidae)				
		(Staphylinidae)	0.50	2.75	1.33	27.50
	Ants	Iridomyrmex sp. (mattiroloi gp)	9.13	2.00	1.27	29.62
		Paratrechina sp. (obscura gp)	2.88	0.63	1.34	23.49
		Pheidole sp.	0.13	16.25	0.61	21.51
November 2002	Spiders	<i>ldiospunna 'fusca'</i> sp. nov. (Corinnidae)	2.00	0.25	1.38	9.97 [`]
		(Gnaphosidae)	4.00	1.63	1.19	8.75
		<i>Grymeus yanga</i> Harvey (Oonopidae)	2.00	1.13	1.34	8.27
	Beetles	(Anobiidae)	6.13	0.50	1.25	23.51
		<i>Brachypeplus</i> sp. (Nitidulidae)	2.38	0.75	1.35	14.10
	Ants	Paratrechina sp. (obscura gp)	3.75	21.75	1.53	28.98
		lridomyrmex sp. (mattiroloi gp)	15.88	5.25	0.95	17.98
		Rhytidoponera metallica (Smith)	13.75	3.25	1.67	17.80

Table 3.4. Repeated-measurFactorSampling timeErrorDistance to logDistance to log× sampling tiError a data arcsine transformed" $P \leq 0.005$

		% leaf litter cover ^a	
	d.f.	MS	F
	1	0.00	0.01
	6	0.41	-
	5	0.59	21.75**
time	5	0.00	0.11
	30	0.03	_

Table 3.4. Repeated-measures analysis of variance of % leaf-litter cover.

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
α	Coefficient for autumn/winter sampling	-0.917 ± 0.096	-1.065,-0.687	0*
βı	Coefficient for brief/no flooding	2.689 ± 0.097	2.509, 2.887	1.0*
βz	Coefficient for medium flooding	$\textbf{2.711} \pm \textbf{0.117}$	2.468, 2.904	1.0*

Table 3.5. Critical parameter details for the Bayesian analysis of spider abundance[#](16 sites).

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β_3	Coefficient for extended flooding	2.596 ± 0.089	2.441, 2.757	1.0*
γ	Coefficient for fallen-timber load	0.001 ± 0.002	-0.002, 0.004	0.79

Ş

[#] ln(x +1) transformed

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				bəmioisn	# n(x+1) tra
	0.64	-0.008, 0.010	\$00.0 ± 100.0	Coefficient for fallen-timber load	Ĺ
	*0`1	4.813, 5.811	122.0 ± 405.2	Coefficient for extended flooding	દ્ધ
	*0*1	886's 'LLI's	90 2 .0 ± 1 2.2	Coefficient for medium flooding	ζď
	*0'1	205.9,502	822.0 ± 679.2	Coefficient for brief/no flooding	'g'
<u> </u>	*0	-5.846, -2.056	661'0 T ZS4'Z-	Coefficient for autumn/winter sampling	Ø
ssem	Posterior probability	95% credible interval	Mean±SD	Description	Parameter

Table 3.7. Critical parameter details for the Bayesian analysis of ant abundance[#](16 sites).

Table 3.6. Critical parameter details for the Bayesian analysis of beetle abundance [#] (16 sites).	
	-

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
α	Coefficient for autumn/winter sampling	0.954 ± 0.144	0.671, 1.222	1.0*
βı	Coefficient for brief/no flooding	2.496 ± 0.105	2.306, 2.691	1.0*
B2	Coefficient for medium flooding	2.541 ± 0.185	2.142, 2.833	1.0*

β_3	Coefficient for extended flooding	3.067 ± 0.130	2.825, 3.382	1.0*
γ	Coefficient for fallen-timber load	-0.006 ± 0.003	-0.010, 0	0.03*

[#] ln(x +1) transformed

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
α	Coefficient for autumn/winter sampling	-0.108 ± 0.093	-0.285, 0.073	0.13
β_l	Coefficient for brief/no flooding	1.724 ± 0.115	1.500, 1.951	1.0*
B2	Coefficient for medium flooding	1.713 ± 0.087	1.533, 1.886	1.0*

Table 3.9. Critical parameter details for the Bayesian analysis of species richness of beetles (16 sites).

Table 3.8. Critical parameter details for the Bayesian analysis of species richness of spiders (16 sites).

٨	Coefficient for fallen-timber load	700 . 0 ± 0	-0.004, 0.003	0.42
rg/	Coefficient for extended flooding	£01.0 ± 668.1	760.2 ,283.1	*0'I
ζď	Coefficient for medium flooding	2.024 ± 0.077	1.862, 2.175	*0.1
'Ø	gnibooft on/feird rot tneisifteoD	201.0 ± 159.1	041.2,047.1	*0'1
Ø	Coefficient for autumn/winter sampling	III'0∓968'0-	-1.127, -0.680	*0
Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

β_3	Coefficient for extended flooding	1.993 ± 0.104	1.792, 2.193	1.0*
Y .	Coefficient for fallen-timber load	0±0.002	-0.003, 0.004	0.55

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
α	Coefficient for autumn/winter sampling	-0.520 ± 0.073	-0.670, -0.385	0*
βı	Coefficient for brief/no flooding	2.235 ± 0.114	1.979, 2.447	1.0*
β2	Coefficient for medium flooding	2.002 ± 0.090	1.825, 2.179	1.0*
ß.	Coefficient for extended flooding	1.750 ± 0.125	1.515, 1.978	1.0*

Table 3.10. Critical parameter details for the Bayesian analysis of species richness of ants (16 sites).

		rda zo ora funum		
Posterior probability mass	95% credible interval	Mean ± SD	Description	Parameter
*0	-1.847, -1.126	981'0∓16†'1-	Coefficient for autumn/winter sampling	<u>n</u>
*0'1	5.430, 3.496	3.013±0.262	Coefficient for briefino flooding	'g'
*0'i	5.020, 3.476	69£.0±0£9.2	Coefficient for medium flooding	ζď
*0.1	2:568, 3.238	181.0±788.2	Coefficient for extended flooding	٤J
15.0	\$10.0 ,610.0 -	- 00.0±100.0-	Coefficient for fallen-timber load	λ

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

bernofsnart $(1 + x)nl^{*}$

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
α	Coefficient for autumn/winter sampling	1.183±0.243	0.706, 1.653	1.0*
β_l	Coefficient for brief/no flooding	2.453±0.339	1.826, 3.047	1.0*
β_2	Coefficient for medium flooding	2.771±0.421	1.782, 3.445	1.0*
ß,	Coefficient for extended flooding	3.032±0.223	2.593, 3.410	1.0*

Table 3.12. Critical parameter details for the Bayesian analysis of beetle abundance[#](8 sites).

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Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
ø	Coefficient for autumn/winter sampling	255.0±002.2-	-5.883, -1.529	*0
ſſ	Coefficient for brief/no flooding	204.0±264.2	4.559, 6.512	*0.1
zđ	Coefficient for medium flooding	404.0±628.4	4.027, 5.650	*0°I
ťď	Coefficient for extended flooding	0\$£.0±121.2	048.2 ,724.4	*0.1
h	Coefficient for fallen-timper load	110.0±£00.0-	610.0 , 610.0-	14.0

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

* In(x+1) transformed

γ

Coefficient for fallen-timber load

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[#]ln(x +1) transformed

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

Posterior probability mass	95% credible interval	Mean ± SD	Description	Parameter
<u> </u>	\$6£.0 ,225.0-	6\$1.0±260.0	Coefficient for autumn/winter sampling	ø
*0.1	1164, 2.080	\$\$2.0 1 ,589±0.23¢	Coefficient for brief/no flooding	'g
*0.1	955.2 ,507.1	202.0±220.2	Coefficient for medium flooding	<i>tg</i>
*0.1	1.744, 2.397	2.085±0.165	Coefficient for extended flooding	۶đ
0.23	-0.012, 0.009	200.0±£00.0-	Coefficient for fallen-timber load	٨

Table 3.15. Critical parameter details for the Bayesian analysis of species richness of beetles (8 sites).

Table	3.14.	Critical	parameter de	etails	for the	he Ba	ayesian	analysis	s of spec	cies ric	hness of	spiders	(8 sites).
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			05% andible internal	Posterior probability mass
Parameter	Description	Mean \pm SD	95% credible micryar	rostenor probability mass
α	Coefficient for autumn/winter sampling	-0.871±0.212	-1.290, -0.446	0*
βι	Coefficient for brief/no flooding	1.992±0.176	1.675, 2.392	1.0*
β_2	Coefficient for medium flooding	2.119±0.150	1.824, 2.407	1.0*
ß	Coefficient for extended flooding	1.973±0.133	1.703, 2.213	1.0*

p_s	Coomorone for outended abovenB			
γ	Coefficient for fallen-timber load	0.003±0.004	-0.005, 0.013	0.78





Pitfall trap 0



characteristics influenced by the log



Table 3.16. Critical parameter details for the Bayesian analysis of species richness of ants (8 sites).

FOSIERIOF PRODUCTY MASS	иссенове инстрато в	Mean ± SD	นอนประวา	rarameter
 *0	-0.630, -0.126	££1.0±276.0-	Coefficient for autumn/winter sampling	ø
*0'1	1.894, 2.719	161.0 1 746.2	Coefficient for brief/no flooding	ľď
*0.1	1.621, 2.383	2.028±0.184	Coefficient for medium flooding	zØ
*0'1	1.414, 2.013	1\$1.0±917.1	Coefficient for extended flooding	۴g
62.0	+10.0 (200.0-	200.0±400.0	Coefficient for fallen-timber load	٨

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

Figure 3.1. Capacity of different sampling designs to measure effects of fallen timber at different scales. Darker shading denotes areas with more intense local processes.

la-b. Randomly placed traps differentiate between the 'mean' effect of local processes at sites with high and low loads of fallen timber when the strength of the influence of small-scale processes on biodiversity is the same per log across sites.

2a-b. Randomly placed traps fail to differentiate between the 'mean' effect of local processes at sites with high and low loads of fallen timber when the contribution to biodiversity differs per log across sites.

3a-b. Traps placed adjacent to logs determine if individual logs make a different contribution to local promotion of biodiversity between areas with different levels of fallen timber.

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Figure 3.2a. Mean (\pm SE) change in total abundance and species richness of

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Figure 3.2c. Mean (\pm SE) change in abundance and species richness of beetles with proximity to logs at the four sampling times.

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Figure 3.3. Mean (\pm SE) change in % leaf litter cover with distance from

CHAPTER FOUR

EFFECTS OF MANAGED FLOODING ON GROUND-ACTIVE BEETLES (COLEOPTERA) AND SPIDERS (ARANEAE) IN RIVER RED GUM **EUCALYPTUS CAMALDULENSIS FOREST**

Abstract

The flood pulse is considered to drive the productivity and ecology of river-floodplain systems in tropical and temperate regions. River regulation reduces the frequency and predictability of flooding. The capacity of flood-adapted invertebrates to cope with these changes in flood regime largely is unknown. In this study, the current and historic hydrophilic invertebrate fauna in river red gum *Eucalyptus camaldulensis* floodplain forest was characterized. The hydrophilic beetle and spider fauna was found to share many traits with counterparts from temperate floodplains elsewhere, including high mobility and flexible habitat requirements. Environmental variability, rather than unpredictability, might be the predominant selective pressure for these traits and thus, the evolutionary impacts of regular and unpredictable flood pulses may be more similar than was recognized previously. Some species displayed high levels of habitat fidelity to temporary wetland habitat and populations of those species are likely to be vulnerable to reduction in habitat availability arising from river regulation.

Beetle and spider assemblages were surveyed for two years after a managed flood to assess short- and long-term impacts of flooding on biodiversity. In the short-term, an influx of large, hydrophilic ground beetles into flood-affected areas increased total beetle biomass by two orders of magnitude relative to dry sites. Flooding was associated with a sustained increase in species richness of beetles and did not reduce species richness of spiders. There was no consistent evidence for convergence of the fauna between flood-affected and dry areas with increasing time elapsed since flooding. Persistent flood-associated change in habitat structure might account for long-term differences in the composition of invertebrate assemblages between areas subjected to different durations of inundation. Thus, relatively unpredictable flood pulses in regulated river systems have a substantial impact on the productivity and ecology of floodplain fauna. Therefore, the Flood Pulse Concept is a useful model for understanding of the ecology of floods created by environmental flows in regulated river-floodplain systems and managed flooding is an effectual means to promote biodiversity.

Introduction

The effects of floods on aquatic taxa inhabiting river channels are well documented, largely because lotic systems long have been used as models for studies of disturbance impacts (e.g. Reice 1985; Resh *et al.* 1988; Lancaster 1996; Lake 2000). In contrast, Junk (1996) considered the development of a conceptual framework for understanding floodplain ecology to be in the preliminary stages. Floodplains are dynamic interfaces that fluctuate between aquatic and terrestrial phases and, thus, contain species belonging to both aquatic and terrestrial environments, as well as species typical of humid zones (Pinay *et al.* 1990; Junk 1997).

The Flood Pulse Concept (FPC) currently is the most influential paradigm in floodplain ecology. The FPC promulgates the view that rivers and their floodplains are components of a single, integrated system (Tockner *et al.* 2000). The model emphasizes the ecological importance of habitat heterogeneity and lateral connectivity between the river channel and the floodplain (Junk 1989 *et al.*; Tockner *et al.* 2000). The FPC largely was based on tropical river-floodplain systems where flooding is highly predictable. The original model was not considered applicable to river-floodplain systems with unpredictable flooding. Tockner *et al.* (2000) later conceded that " 'stochastic events' are fundamental...for maintaining biodiversity in temperate floodplains," and revised the model to better incorporate temperate river-floodplain systems.

Flows in Australian river-floodplain systems naturally are highly variable (Lake 1995; Walker *et al.* 1995). Moreover, river regulation has reduced the predictability of floods in temperate Australia by removing the peak in flow created by the spring snowmelt (Bren *et al.* 1987). The applicability of the FPC to unpredictable systems remains contentious. Tockner *et al.* (2000) asserted that "general predictions on the ecological 'benefit' of episodic expansion-contraction events are not yet possible." In contrast, Walker *et al.* (1995) contended that the FPC could be a useful model for understanding dryland river-floodplain systems where flooding is unpredictable. Both Junk *et al.* (1989) and Walker *et al.* (1995) viewed unpredictability as a barrier to the exploitation of the flood pulse by organisms. However, few studies have measured the floodresponse of biota on floodplains where inundation is naturally unpredictable or has become unpredictable as a result of river regulation (but see Ellis *et al.* 2001; Bonn *et al.* 2002).

Many of the same invertebrate families occur on floodplains in tropical, temperate and dryland regions, despite differences in the predictability of flooding between these climates. The Carabidae (ground beetles) and Lycosidae (wolf spiders) contain many hydrophilic species that are specialized inhabitants of the land-water interface. Ground beetles and wolf spiders are predators that inhabit floodplain ecotones worldwide. In Europe, it is well established that certain ground beetles are highly adapted to the floodplain environment (Theile 1977; Zulka 1994; Siepe 1995). In Australia, many species of ground beetles and wolf spiders are yet to be described and ecological research on terrestrial hydrophiles is nascent (New 1998; but see Framenau 2002). There is no reason to presuppose that Australian ground beetles and wolf spiders lack the capacity to employ adaptive strategies used by their relatives on temperate or tropical floodplains elsewhere.

An appreciation of the response of floodplain fauna to inundation is necessary to assess the level of flood adaptation and the ecological 'benefits' of flooding. Studies of floodplain biota have tended to substitute spatial replication for long-term sampling, so little is known about the time scales over which flooding influences biota (e.g. Uetz *et al.*1979; Nilsson and Jansson 1995; Bell *et al.*1999). Few studies have tracked postflood successional trajectories to determine if the biota from flooded areas does actually become more like the biota from unflooded areas with increasing time since the flood disturbance (but see Pautau *et al.* 1997; Molles *et al.*1998).

Understanding the level of flood-adaptation in the floodplain fauna on regulated rivers has important conservation and management implications. Most of the large rivers in south-eastern Australia are regulated and comprehending how different flow regimes affect biodiversity is a major challenge for ecological management. In south-eastern Australia, river red gum *Eucalyptus camaldulensis* Denhn. forms extensive floodplain forests along some rivers. Barmah Forest is the largest extant river red gum floodplain forest, covering ca 29 500 ha and extending up to 10 km from the main river channel.

Barmah Forest is sub-humid to semi-arid, receiving ca 400 mm rainfall per year. Invertebrates living on the floodplain away from river margins must be able to tolerate low humidity during the dry phase and high temperatures. Barmah Forest is approximately 10 000 years old (Bowler and Harford 1966)—a short period in evolutionary time.

Barmah Forest naturally flooded as a result of winter rainfall and spring snowmelt. Since river regulation, flows have become more unpredictable (Bren *et al.* 1987). In 1993, Barmah Forest was allocated an annual Environmental Water Allocation (EWA) of 100 GL (Barmah-Millewa Forum 2001). However, release of the EWA is contingent on hydrological triggers and consequently, the EWA first was used to create extensive flooding of Barmah Forest in spring/summer 2000–2001. Floodwaters peaked in November 2001, which is later in the year than would be usual for natural flooding (Barmah-Millewa Forum 2001). Studies of biotic responses to managed flooding have focused on fish and vegetation (e.g. Bayley 1991; Bovee and Scott 2002). Little attention has focused on the response of invertebrates to managed flooding (but see Ellis *et al.* 2001; Stevens *et al.* 2001).

Here, I document the response of ground-dwelling beetle and spider assemblages to managed flooding over 32 mo in Barmah Forest to determine whether faunal responses to flooding in this highly variable and unpredictable environment are consistent with patterns observed on floodplains with more predictable flood regimes. Records of the floodplain fauna of the Murray River before river regulation are collated to ascertain whether present-day assemblages are representative of the 'natural' fauna. The influence of duration of inundation on beetle and spiders assemblages is described. The capacity of river-channel margins and moira-grass *Pseudoraphis spinescens* (R. Br.) wetlands to function as habitat for hydrophilic taxa was measured to assess the vulnerability of species to population declines associated with reduction in flooding. Last, the persistence of faunal changes initiated by flooding was measured over a 2-yr period to determine whether the fauna on flooded areas converged with fauna from unflooded areas when sufficient time elapsed since flooding.

Methods

Study area

This work was conducted in Barmah State Forest and Barmah State Park in northern Victoria, Australia, about 215 km from Melbourne (35°55'S 145°08'E). Barmah Forest occurs on the Murray-River floodplain where the channel has unusually low capacity. The Murray River and many anastomosing creeks run through the forest.

Soils are stratified layers of clay overlaid by sand (Silvers 1993). Barmah Forest consists largely of monospecific stands of *Eucalyptus camaldulensis* with an understorey of grasses, rushes and sedges (Chesterfield 1986). Flood-prone, treeless plains dominated by semi-aquatic moira grass *Pseudoraphis spinescens* occupy about 5% of Barmah Forest (Chesterfield 1986). These areas flood for an average of 4.9 mo in 75% of years, although encroachment of river red gums on to the moira-grass plains has been linked to changes in the natural flood regime resulting from river regulation (Bren 1992).

Under natural flood regimes, high flows created by austral winter rainfall and spring snowmelt regularly fully flooded the forest (Bren 1988). Substantial regulation of the Murray River began in 1934 with the construction and filling of the Hume Dam at Albury, ca 300 km upstream from Barmah Forest. Regulation has reduced the frequency of flows associated with partial forest flooding and shifted the timing of flooding to increased occurrence of smaller summer floods and a reduction in winter and spring floods (Bren 1938).

Site selection and flooding of the study area

In May 2000, an initial $1550 \text{ m} \times 50 \text{ m}$ study sites were selected throughout Barmah Forest. This study was originally designed to explore effects of fallen timber on fauna. Consequently, study sites were selected to have either high (> 50 t ha⁻¹) or low (< 20 t ha⁻¹) fallen-timber loads. In January 2001, eight additional sites were selected in areas with high fallen-timber loads. Exploration of the influence of flooding on invertebrate assemblages was largely opportunistic and there is some confounding of study design because sites that had higher levels of fallen timber also were more flood-prone. The duration of flooding occurring at each site could not be predicted when the sites were selected. Five of the low fallen-timber sites experienced brief or no flooding and the remaining three experienced moderate flooding. Two high fallen-timber sites flooded briefly or not at all, five flooded moderately and the remaining nine flooded for an extended period. However, I concluded that fallen-timber load had little influence on invertebrate fauna at the site scale (Chapter Three). Therefore, the potential influence of fallen timber is not considered in this chapter.

The last major floods in Barmah Forest before 2000–2001 were in 1992–1993, with less-extensive flooding occurring in 1996 (Barmah-Millewa Forum 2001). In the austral spring/summer 2000–2001, Barmah Forest experienced widespread flooding with much of the forest inundated by October 2000. Large tracts of forest remained inundated for several months, prohibiting sampling in November 2000. Floodwaters receded by January 2001.

Because the level of flooding experienced at each study site was not directly measured, a *post facto* measure of inundation was devised. Study sites were rated as having experienced 'brief,' 'moderate' or 'extended' flooding based on the following suite of site characteristics:

(i) brief or no flooding: soil dry and compacted, ground cover of dry grasses, no aquatic-insect pupal cases evident;

(ii) moderate flooding: soil dry, ground covering generally of verdant grass
but may be some dead aquatic plants present, few aquatic-insect pupal cases present,
may be some silt deposited by floodwaters evident;

(iii) extended flooding: damp soil, considerable growth of water plants, many pupal cases of aquatic insects attached to tree trunks, often extensive silt deposition, 'watermark' left on tree trunks.

The following year, spring/summer 2001–2002, flooding in Barmah Forest was negligible and none of the study sites or their immediate surrounds were inundated. In spring/summer 2002–2003, moderate flooding occurred with three study sites being inundated partially by the November sampling period. Unfortunately, floodwaters prevented access to one of the sites, so data from only two re-flooded sites were collected. By January 2003, floodwaters had receded and one further study site showed evidence of very brief flooding. Thus, four sites were categorized as experiencing a second flood, although the immersion phase was considerably shorter than in 2000–2001 (Fig. 4.1).

To identify potential sources of hydrophilic colonists of flooded forest-floor sites, invertebrates were sampled at sites with permanent or more regular water. Invertebrates were sampled at seven sites on channel edges (three on the Murray River and four along creek margins). Study sites along the main channel were situated in places where the bank had a gentle gradient to the water's edge, rather than in places where the bank was steep. Two sites on the moira-grass plains, where conditions are essentially lentic, also were sampled. Water birds frequently interfered with the pitfall traps on the moira-grass wetlands, necessitating frequent clearing and resetting of the traps. Consequently, it was logistically impossible to maintain more lentic sites than this number. To ensure that the hydrophilic species that colonized sites after extended flooding during spring/summer 2000–2001 still were present in the forest, an area of forest floor that experienced extended inundation in spring-summer 2002–2003 was sampled in that year.

Sampling protocol

Sampling was conducted at the initial 16 sites in May 2000 and concurrently at all 24 sites in January 2001, May 2001, November 2001, January 2002, November 2002 and

January 2003, as well as at the additional channel-edge, moira-grass wetland and forestfloor sites in November 2002 and January 2003. Sites also were sampled in August 2000 and August 2001, but very few spiders and beetles were trapped and the data were excluded from further consideration.

Five pitfall traps with an opening diameter of 75 mm and depth 95 mm were set on each study site. Traps were closed for ≥ 24 h following installation to counter possible 'digging-in' disturbance effects (Greenslade 1973). Pitfall traps then were filled with a 70% propanol: 5% glycerol: 25% water solution and opened for five days and nights. When returned to the laboratory, samples were sieved to 1 mm² and transferred to a 70% ethanol: 30% distilled water solution for storage. Specimens were sorted to morphospecies, which then were identified to the highest practicable taxonomic level. Expert taxonomic assistance was sought (see acknowledgements).

Determining the dry mass of specimens using oven-drying methods damages specimens. In the current study, I wished to maintain the specimens in good condition to enable samples to be double-checked and to preserve some specimens for lodgement in museum collections. Furthermore, the specimens had been in ethanol for some months before being processed. Fatty acids are soluble in ethanol, resulting in gradual reduction in body mass of stored specimens (Mason et al. 1983). Therefore, use of regression equations to estimate body mass from body length was preferred to the ovendrying method. The body length of the voucher specimens for each species trapped in January 2001 was measured using a digital caliper, to 0.02 mm precision, while the specimen was viewed through a binocular microscope. Body length excluded appendages such as antennae, ovipositors, wings and spinnerets (Hódar 1996). Where multiple specimens were available for a morphospecies, three individuals were measured and the mean of the body lengths recorded. The equations of Hódar (1996) were used to convert body length to approximate body mass. Beetles have a diverse range of body forms and, where possible, equations specific to individual beetle families were used. Faraily-specific equations were not available for the minor families, so a general coleopteran equation was applied to some specimens. A single conversion equation was used for all spiders.

Literature search

The literature was searched for records of the historic distributions of spiders and beetles on the central Murray-River floodplain. Only ground beetles (Carabidae) were found to have been collected extensively and described from the region before river regulation, so the search focused on collating records for that family. Some additional records of ground beetles on the Murray River made after river regulation also were collected. Natural-history information and more recent records of both ground beetles and wolf spiders were compiled to allow shared characteristics of the floodplain species to be identified. A preliminary examination of The Museum of Victoria's ground-beetle collection was conducted for specimens collected from the region, but the search was abandoned because there were so few well-labelled specimens.

Data analysis

To aid visual recognition of possible faunal patterns, the abundance and species richness of all beetles and spiders, as well as the proportion of the fauna comprised by each major family, was plotted for each survey period. Ground beetles and wolf spiders were recognized a priori as potentially responsive to flooding so mean abundance of those taxa at sites experiencing different flood regimes also was plotted against time since flooding. Non-parametric Mann-Whitney-Wilcoxon tests were used to compare the abundance of ground beetles and wolf spiders between different groups of sites because it was not possible to know if the data were normally distributed.

Relationship between flood duration and invertebrate abundance and species richness

The study was a repeated-measures design, with seven visits to the same study sites. However, eight sites were not visited until the second survey time (January 2001). Furthermore, three sites and four sites had to be excluded from the November 2002 and January 2003 analyses respectively because they flooded a second time. Frequentist repeated-measures ANOVA designs do not deal well with large amounts of missing

data, particularly when the data are missing in a fairly systematic fashion, as was the case here (Quinn and Keough 2002). In this study, data from flood-prone sites were more likely to be missing from the last two sampling periods than data from drier sites. Bayesian analyses are amendable to utilizing all data, so these were used here. The Bayesian models were run using the WinBUGs (Version 1.4, Spiegelhalter et al. 2003) program, which computes the joint posterior probability distributions of the model parameters with the data. Uninformative, normally distributed priors were used.

To analyze the effect of the 2000-2001 floods on the abundance of beetles or spiders at sites subject to different durations of inundation, I used this model:

$Y_{j(i)k} \sim \text{Normal}(\mu_{jk}, \sigma_{jk})$

Y is the natural logarithm of (number of beetles or spiders +1) caught at study site *i* at sample time k, where the duration of inundation experienced in spring/summer 2000-2001 at study site j is denoted by i. l represents the 'season' (i.e. warm or cold months) during which the sample was collected. α models the effect of sampling in the cooler months on Y, and λ are elements of a matrix that identifies survey as being conducted in the cooler months (May) ($\lambda = 1$) or the warmer months (November, January) ($\lambda = 0$). The β s model the effect of duration of local flooding in spring/summer 2000–2001 on Y, and π are elements of a matrix that identify sites as belonging to a particular flood treatment (brief, moderate or extended inundation). σ_i are site random effects, while the σ_{ik} are site-repeated-survey random effects (Breslow and Clayton 1993).

To determine whether there was an overall difference in beetle or spider abundance between sites subject to different durations of inundation in 2001, pairwise differences in β s were calculated. These calculations are analogous to *post hoc* pairwise comparisons in frequentist statistics, but without the interpretative complications involved with adjustment of type-I error rates.

 $\mu_{i(i)k(l)} = \alpha_l \lambda_{k(l)} + \beta_i \pi_{i(l)} + \sigma_i + \sigma_{ik}$

The overall pairwise comparisons potentially could obscure short-term differences created by flooding. To track the strength of flood response through time, the mean difference in *Y*s between flood treatments for each survey time $\mu_{\delta Yk}$, was calculated by:

 $\mu_{\delta Yk} = 0.33 \times ((Y_{j=1k} - Y_{j=3k}) + (Y_{j=1k} - Y_{j=2k}) + (Y_{j=2k} - Y_{j=3k}))$

where:

- j=1 denotes sites subject to brief/no inundation;
- j=2 denotes sites subject to moderate inundation;
- j=3 denotes sites subject to extended inundation

A variation on the model was used to examine the effect of flooding and season on the species richness of beetles or spiders. Because species richness is likely to be Poisson distributed (i.e. consisting of small, non-negative integers), it was necessary to include a logarithmic link function in the model such that:

 $Y_{j(i)k} \sim \text{Poisson} (\mu_{jk})$ $\ln(\mu_{j(i)k(l)}) = \alpha_l \lambda_{k(l)} + \beta_j \pi_{j(i)} + \sigma_j + \sigma_{jk}$

Relationship between invertebrate biomass and flood duration

A Bayesian model was fitted to the January 2001 data for (1) mean body mass of specimens and; (2) the total biomass of the catch. The model used was:

 $Y_{j(i)} \sim \text{Normal} (\mu_j, \sigma_j)$ $\mu_{j(i)} = \beta_j \pi_{j(i)} + \sigma_j$

Where Y is the natural logarithm of the mean body mass of specimens or total catch biomass at study site j with j(i) denoting the duration of inundation that study site j experienced in spring/summer 2000-2001. The π are elements of a matrix that identifies the site as belonging to a particular flood treatment (brief, moderate or extended inundation). The σ_i are site random effects (Breslow and Clayton 1993). For all model outputs, the mean, standard deviation and 95% credible intervals for the model parameters of interest, (α , β and μ_{57R}) were derived. Bayesian statistics has no hard-and-fast conventions for making decisions about what constitutes a 'substantial' effect. Nevertheless, a decision-making criterion is useful for identifying 'important' factors. In the current study, I adopted the simple decision-making criterion of Mac Nally and Horrocks (2002). Bayesian analysis provides a posterior probability distribution for each of the model parameters (and combinations thereof, such as the difference between any two parameters). The proportion of the posterior probability distribution lying above zero is referred to as the posterior probability mass (PPM). When a model parameter has no effect on the dependent variable, the posterior probability distribution is centred on zero and the expected value of PPM is 0.50. Model parameters with \geq 90% of the posterior probability distribution lying above zero, i.e. PPM \geq 0.90, were considered to have a 'substantial' positive effect on the dependent variable. For parameters with negative coefficients, \geq 90% of the posterior probability distribution must lie below zero to be classed as 'substantial,' giving a PPM \leq 0.10.

Changes in invertebrate assemblage composition over the three-year study period with reference to flood response

The PRIMER statistical package (Version 5, Clarke and Gorley 2001) was used to compute Bray-Curtis similarities from morphospecies-by-site matrices. The choice of data transformation prior to computation of similarity matrices is determined by the relative weighting a researcher wishes to give to rare and abundant species (Clarke and Warwick 1994). The results presented here are from square-root transformed data. This transformation moderately reduces the influence of highly abundant species. However, the analyses were done using a variety of transformations and the results differed little.

Analyses of similarities (ANOSIMs) were computed, each using 20 000 iterations, with assemblages grouped by duration of flooding in spring/summer 2000–2001. Both pairwise and global test statistics were calculated. Similarity percentages analyses (SIMPER) were performed to identify influential species contributing to differences in

assemblages between sites for January 2001 (immediately post-flood) and for January 2003 (2 yr post-flood).

Habitat range of hydrophiles

To determine whether the fauna collected on recently flooded forest-floor sites was likely to have originated on channel edges and/or in moira-grass wetlands, ANOSIMs were used to compare assemblages between channel edges, moira-grass wetlands and recently emersed areas of forest floor. Data from forest-floor sites January 2001 and from sites that re-flooded in January 2003 were treated as separate, independent groups. A ratio of mean between-group dissimilarity to standard deviation for individual species can be used as a measure of the consistency of the distribution/habitat affiliation patterns. Clarke and Warwick (1994) considered a ratio ≥ 1.4 to represent high habitat fidelity. The PRIMER package (Clarke and Gorley 2001) does not test formally whether a given dissimilarity mean/standard deviation ratio is likely to be the result of a non-random distribution of individuals of that species between habitats. The IndVal computer program (Version 2.0, Dufrêne and Legendre 1997) uses an algorithm to calculate a habitat-fidelity score from the species distribution data and then performs a randomization test to determine the probability of getting an equivalent habitat-fidelity score with random distribution of the species among habitat types. Consequently, the IndVal package was used to calculate an index of habitat fidelity for each ground-beetle and wolf-spider species for which ≥ 20 specimens were collected such that:

Habitat fidelity to habitat X = proportion of sites in habitat X occupied x mean abundance in habitat X/(mean abundance in habitat X+ mean abundance in habitat Y).

The IndVal package automatically calculates the habitat fidelity index for the habitat type to which each species was most faithful. Sites were divided into temporary-wetland sites and channel-edge sites. Temporary-wetland sites constituted the forest-floor sites subjected to moderate or extended inundation in 2001 or 2003 and the moiragrass wetland sites. Channel-edge sites were the sites on the banks of the Murray River and the anastomosing creeks. A randomization test with 500 iterations was used to decide whether individu and channel-edge sites.

decide whether individuals were randomly distributed among temporary-wetland sites

Results

Literature search

At the turn of the twentieth century, the prolific taxonomist, Thomas Gibson Sloane, collected ground beetles in the Riverina and the rough distribution notes, accompanying his formal descriptions of new species, provided the basis for the comparison with present-day assemblages of ground-beetles on the floodplain (Table 4.1 and 4.2). (The Riverina district comprises 90 000 km² of the Murray-Darling Basin in south-western New South Wales and north-central Victoria, including Barmah Forest.) Several of the species of ground beetle captured in the current study were known to be present in the region before river regulation was established (Tables 4.1 and 4.2). Sloane (1896) described a suite of species from the fossorial, hydrophilic genus *Clivina* (Carabidae: Scaritinae) as characteristic of the Riverina district (Table 4.2). Five species of *Clivina* trapped by Sloane (1896) also were recorded in the present study. Thus, the species composition of current-day assemblages bears some resemblance to the floodplain fauna before river regulation. However insufficient published records exist to make any definitive statements about long-term change in the Murray-River floodplain fauna (Tables 4.1 and 4.2). M. Baehr (Zoologische Staatssammlung Münchhausenstraße) will re-examine Sloane's collection in February 2004, possibly enabling compilation of a more comprehensive historic species list. The ground beetles and wolf spiders now present on the floodplain and channel edges are characterized by wide distributions and the capacity to tolerate environmental variability (Table 4.1). Moore (1976) observed that the invasive South American species Bembidion brullei (Gemminger and Harold) had become widespread in the Murray-Darling Basin (Table 4.1), but no introduced ground beetles were recorded in the present survey.

Relationship between flood duration and invertebrate abundance and species richness —beetles

A total of 6691 beetles from 212 morphospecies and 42 families were captured in pitfall traps, including all 294 beetles caught on channel margins and in moira-grass wetlands in January 2003, as well as 322 carabid beetles caught on channel margins and in moiragrass wetlands in November 2002 (Appendix 4.1). Beetle abundance was higher during the autumn surveys compared to the late-spring and mid-summer surveys (Table 4.3, Fig. 4.2). This difference was due largely to very high abundance of a single litterdwelling species, Nargomorphus sp. (Leiodidae: Cholevinae), in autumn. Beetle abundance did not differ substantially among sites in relation to local flood regime (differences in β -coefficients), when all the data were combined into a single model. However, when each survey was considered separately, beetles exhibited a gradient of increasing abundance with duration of localized flooding for all of the late-spring and summer surveys, but not for the autumn surveys (Table 4.4, Fig. 4.2). It was not possible to definitively establish causality between flooding and greater beetle density because no data from spring or summer before flooding were collected and beetles always were more abundant at more flood-prone sites in the warmer months, even 24 mo after flooding.

Species richness of beetles did not differ much seasonally, despite more beetles being caught in autumn (Table 4.5, Fig. 4.3). Species richness of beetles was greater at sites subject to the longest duration of inundation in spring/summer 2000–2001, relative to sites that experienced moderate or brief/no inundation (Table 4.5, Fig. 4.3). This relationship held for all survey times, even before the 2000–2001 flood (Table 4.6).

Ground beetles (Carabidae) were a major component of the fauna only at forest sites that recently had experienced extended flooding, when they comprised 64% of beetle fauna (Fig. 4.4a and b). At other times, Staphylinidae was the most abundant family of predatory beetles (Fig. 4.4a and b). The beetle fauna often was dominated by detritivorous species, such as certain nitidulids and leiodids (Fig. 4.4a and b).

Sampling of the two accessible, re-flooded sites in November 2002, when floodwaters covered part of the sites, provided an opportunity to establish more clearly the link between flooding and increased abundance of ground beetles. In November 2002, ground beetles were more abundant on sites that had re-flooded compared to other study sites (Fig. 4.5) (Mann-Whitney-Wilcoxon test, $n_{\text{re-flooded}} = 2$, $n_{\text{not reflooded}} = 21$, U = 0, $P \approx$

0.01). The combined channel-edge, moira-grass wetland and flooded forest-floor sites also supported large populations of ground beetles compared with dry forest-floor sites (Fig. 4.5).

Relationship between invertebrate biomass and flood duration—beetles

Areas of forest floor that recently experienced extended flooding were colonized by high numbers of ground beetles. These beetles typically were large. For instance, specimens of Catadromus lacordairei Boisd. had body lengths up to 35 mm. In January 2001, the mean size of beetles caught at sites that recently had experienced extended flooding was greater than at moderately flooded sites or briefly flooded sites (Table 4.7). Greater numbers of beetles were trapped at the longer-flooded sites (Table 4.4). Given that biomass is a product of beetle size and abundance, the biomass of beetles on areas of forest floor that had been inundated for an extended period increased two orders of magnitude relative to unflooded areas (Table 4.8).

Relationship between flood duration and invertebrate abundance and species richness --- spiders

A total of 2532 spiders from 103 morphospecies and 24 families were captured in pitfall traps, including all 177 spiders caught on channel margins and in moira-grass wetlands in January 2003, as well as 136 lycosid spiders caught on channel margins and in moiragrass wetlands in November 2002 (Appendix 4.2). More mature spiders were trapped during the spring and summer surveys than the autumn surveys (Table 4.9). Flood duration was not related to abundance of spiders overall or at any individual survey time, even immediately after flooding (Table 4.9 and 4.10, Fig. 4.6).

Species richness of spiders was greater in spring and summer than in autumn, possibly due to the larger catches in the warmer months (Table 4.11, Fig. 4.7). Averaged over all surveys, species richness was greater on sites that flooded for a moderate period of time in spring/summer 2000-2001 compared with sites that flooded briefly or not at all, but there was no substantial difference between the extensively flooded and least flooded sites. No differences were found in species richness between flood treatments at any individual survey period (Table 4.12). However, the algorithm used to detect these differences assumes a gradient along flood intensity and would not detect a difference when maximum values were obtained for an intermediate level of flooding.

4.9).

Relationship between invertebrate biomass and flood duration-spiders

Mean spider biomass was greater on the dry or briefly flooded sites relative to the moderately flooded sites and extensively flooded sites (Table 4.13). However, total spider biomass was no greater at dry or briefly flooded sites compared with the extensively flooded sites (Table 4.14).

with reference to flood response-beetles

Wolf spiders (Lycosidae) comprised < 20% of the spider fauna at dry sites but, following flooding, made up 81% of the spiders on sites subject to prolonged inundation (Fig. 4.8a and b). Wolf spiders also constituted a large proportion (61%) of spiders on those sites the following spring, but declined by the summer and did not recover to former levels (Fig. 4.8a and b). Whereas nine species of wolf spider were captured immediately following flooding in January 2001, only three species were captured in November 2001. Knobble spiders (Zodariidae) were the most abundant spiders on dry sites (Fig. 4.8b). In November 2002, wolf spiders also were more abundant on sites that were partially re-flooded, compared to sites that had not flooded since January 2001 (Mann-Whitney-Wilcoxon test, $n_{\text{re-flooded}} = 2$, $n_{\text{not reflooded}} = 21$, U = 2.0, $P \approx 0.03$) (Fig.

Changes in invertebrate assemblage composition over the three-year study period

No significant compositional differences existed in beetle assemblages at sites before flooding. However, immediately following the recession of floodwaters in January 2001, the beetle fauna was different between sites experiencing brief/no, moderate or extended inundation (Table 4.15). Hydrophilic ground beetles were largely responsible for the dissimilarity in beetle assemblages between sites subject to different flooding durations (Table 4.16).

During the next two sampling periods (May 2001, November 2001), the composition of beetle assemblages differed between sites that experienced extended flooding and sites that flooded briefly or not at all during spring/summer 2000-2001 (Table 4.15). No flood-related differences were evident in the beetle assemblages between the moderately flooded and the briefly flooded/unflooded sites and between the extensively flooded and . moderately flooded sites (Table 4.15). There was little difference between the extensively flooded sites and the briefly flooded/unflooded sites in the January 2002 sampling period, suggesting that the effects of flooding on the fauna had attenuated. However, by November 2002, in the absence of further flooding, the assemblages on sites that experienced extended inundation in 2001 diverged from the sites that experienced brief/no inundation (Table 4.15). In 2002, a similar divergence occurred between fauna on sites that experienced moderate and brief/no flooding. In January 2003, 2 yr after flooding, the distribution of litter-dwelling species from families including Cryptophagidae and Laemophloeidae was influential in creating differences in the beetle assemblages between sites that were inundated for different lengths of time (Table 4.17).

Habitat range of hydrophiles-beetles

The beetle fauna along the edges of channels in 2003 differed from the forest-floor fauna in both January 2001 and 2003, for all durations of forest-floor inundation (Table 4.18). The results from comparisons with the moira-grass wetlands were unclear because of low power (i.e. few permutations in the randomization test) (Table 4.18). The fauna at the forest-floor sites that flooded a second time in spring/summer 2002–2003 was not detectably different from the fauna on the sites that experienced brief

flooding or no flooding over spring-summer 2000-2001 (Table 4.18). Both groups of sites only had low numbers of ground beetles by January 2003.

Changes in invertebrate assemblage composition over the three-year study period with reference to flood response--spiders

Patterns in the spider assemblage structure could not be fully explained by the 2000–2001 flood (Table 4.19). The spider assemblage composition consistently differed between groups of sites that experienced extended flooding and brief/no flooding in 2001, even before the flood occurred. However, the pre-flood sample was small, making results potentially less definite. In January 2001, immediately after floodwaters receded, differences in assemblage structure between sites that flooded for different lengths of time largely were due to greater wolf-spider abundance at sites that were inundated for longer (Table 4.20). Conversely, knobble spiders (Zodariidae) were more abundant on drier sites (Table 4.20). In January 2003, knobble spiders again were influential in creating assemblage differences, but small, litter-dwelling species, including a prodidomid and a cyatholipid, also were important (Table 4.21). The results of contrasts between sites that experienced moderate and brief/no flooding and between sites that experienced and moderate flooding were relatively consistent with assemblage differences created by inundation attenuating over time (Table 4.19).

Relationship between forest-floor assemblages following flooding and fauna on channel edges and in moira-grass wetlands

The spider fauna on the forest-floor sites that flooded a second time in spring-summer 2002–2003 was not detectably different from the fauna on the sites that experienced moderate flooding during spring-summer 2000–2001 (Table 4.22). This fauna was indistinguishable from the spider fauna along channel edges in 2003 (Table 4.22). The results from comparisons with the moira-grass wetlands were ambiguous because of

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low power. However, the spider assemblages at forest-floor sites that experienced prolonged inundation appeared to more closely resemble the assemblages from lentic, temporary wetlands than channel edges (Table 4.22).

Habitat range of hydrophiles

Seven species of ground beetles trapped on the forest floor in 2001 also were trapped at a forest-floor sites that experienced extended flooding over spring-summer 2002-2003 (Table 4.23). Three species of ground beetles that were trapped on forest-floor sites in 2001 were present in flooded moira-grass wotlands in January 2003, including the most common species trapped on the forest floor Platycoelus prolixus (Er.) (Table 4.23). Four species trapped on forest-floor sites following flooding in 2001 were trapped in small numbers along channel margins in 2003. However, the most abundant species along channel margins, the bombardier beetle Pheropsophus verticalis Dej., was not trapped on the forest floor (Table 4.23). Four species trapped on the forest floor were not trapped in other habitat types, but all were comparatively rare and might have been detected with greater sampling effort.

Three of the four ground-beetle species, for which the distributions were analysed, showed high habitat fidelity to either temporary wetlands or to channel margins (Table 4.23), whereas only one of the three wolf-spider species showed fidelity to temporarywetland habitat (Table 4.24).

Discussion

floodplain fauna?

River regulation reduces flood predictability and, therefore, is expected to favour species with flexible, opportunistic life-history traits. If these opportunistic species are not adapted specifically to flooding, they might not respond positively to the flood pulse. Thus, when flooding does occur, the ecological 'benefits' (Tockner et al. 2002) of the flood pulse might be reduced or eliminated and the Flood Pulse Concept might not model the system accurately. This study sought to characterize the floodplain biota from a regulated river and to compare the fauna with counterparts on 'natural' floodplains in temperate and tropical regions. It was necessary first to establish whether the present-day fauna resembles the fauna that would occur naturally on the river floodplain.

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Characterizing the historic and current fauna - How opportunistic is the

The Murray River has been regulated for nearly 70 years. It is possible that species most vulnerable to changes in the flood regime have been extirpated from the floodplain assemblages long ago and the species captured during this study represent the fraction of the fauna that was tough enough to survive river regulation or a different fauna that colonized the area after the original fauna was displaced by river regulation. Historical records of ground beetles on the Murray-River floodplain were collated to allow comparison of the present-day fauna with the pre-river regulation fauna. Ground beetles are a comparatively conspicuous and easily collected element of the invertebrate fauna and, therefore, feature more in historical records than other taxa considered in this study. Nevertheless, published historical records of the invertebrate fauna of the Murray-River floodplain are scant, allowing only a broad, presence-absence comparison for some species. Such comparisons are fraught with problems of unequal sampling effort and differences in localities and season. The problems cannot be rectified because precise data on these quantities rarely are provided in the historic records. Sometimes, species descriptions are not adequate even for expert modern taxonomists to reconcile the species name with existing specimens, especially when the type specimen

has been lost. Furthermore, faunal change due to human impacts cannot be distinguished from natural temporal variability.

Despite these problems, historic records did reveal some similarities between the preregulation fauna and today's assemblages (Table 4.1 and 4.2). For example, Sloane (1903) described the ground beetle Loxandrus subiridescens (Macl.) as common on the Murray River, and L. subiridescens was the third most commonly trapped species in the present study (Table 4.1). Five of the *Clivina* species that Sloane (1896) recorded in the Riverina district (Murray and Murrumbidgee Rivers) were trapped in the present study, even though that genus is fossorial in mud and sand generally associated with channel edges, whereas most trapping in the present study was done on the forest floor.

Before river regulation, Sloane (1905; 1915) recognized the Riverina district, incorporating the present study area, as a separate Australian faunal sub-region for beetles. However, Sloane (1915) did not consider the area to have a unique, endemic fauna. "The Riverina district is probably merely part of the eastern marches of the Eyrean sub-region. Its chief distinctive character is the prevalence of immigrant forms from the Bassian and Torresian sub-regions" (Sloane 1915). (Eyrean refers to the extensive arid interior of Australia; Bassian refers to the more humid parts of southern Australia and Torresian refers to the tropic and sub-tropic coast of north-eastern Australia (Matthews 1980).) In the present day, the floodplain fauna is still characterized by the intersection of Bassian and Eyrean elements and the prevalence of highly mobile immigrants.

Despite requiring moist conditions, most of the species of ground beetles and wolf spiders captured on the floodplain can tolerate a range of habitats and consequently, are widely distributed (Table 4.1). Sloane (1896) recognized that the large distances traversed by the Murray River and its tributaries probably aided the distribution of ground beetles across vast areas-an appreciation of habitat connectivity that long predates the modern discipline of landscape ecology. However, common, widespread species are most likely to have been described by taxonomists. During the current study, species were captured that were previously unknown and little can be said about their habitat requirements or distributions. In contrast to high levels of endemism in tropical floodplain forests, invertebrates on floodplains of relatively natural rivers in

unregulated rivers.

In the current study, the most abundant species of beetles on the forest floor following flooding all were fully winged and, therefore, potentially highly mobile. Darlington (1961) considered the high proportion of flying Australian hydrophiles to have evolved in response to aridity and environmental variability at the continental scale. Darlington (1943) noted high proportions of winged carabid beetles in areas with substantial ant faunae, which is true of semi-arid Australia. Floodplain wolf spiders also are highly mobile. Whereas many large lycosid spiders inhabit burrows, which are vulnerable to flooding, the small floodplain species of the genus Artoria are not confined to burrows (Framenau 2002). Moreover, wolf spiders have mobile brood care, enabling eggs and spiderlings to be protected from drowning or desiccation as conditions change (Uetz 1976; Framenau et al. 2002).

High mobility is essential for floodplain hydrophiles, not only to avoid drowning in rising floodwaters (Darlington 1943), but also to rapidly colonize areas left exposed by receding floodwaters in order to exploit stranded aquatic prey. Other studies have highlighted the importance of high dispersal powers to floodplain invertebrate assemblages in both temperate and dryland river systems (Zulka 1994; Ellis et al. 2001; Adis and Junk 2002). In the floodplain forests of tropical Amazonia, maintaining flight enables species to exploit periodically favourable habitat (Adis and Junk 2002). Thus, high mobility is an adaptation to high habitat variability, not necessarily to habitat unpredictability. Similarly, hydrophilic invertebrates on tropical, temperate and dryland floodplains utilize arboreal flood refugia (Zulka 1994; Adis and Junk 2002) (see Chapter Six).

In contrast to some species from temperate floodplains in Europe that spread their reproductive effort over two seasons, species of wolf spiders on the floodplain of an upland river in Victoria have a single reproductive season (Framenau 1998). Framenau

temperate Europe also occur in habitats outside the floodplain and many have wide geographic distributions (Zulka 1994; Adis and Junk 2002). Thus, the habitat requirements of the fauna on the floodplain of the regulated Murray River are flexible, but the level of plasticity seems comparable with counterparts from floodplains of has been lost. Furthermore, faunal change due to human impacts cannot be distinguished from natural temporal variability.

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In contrast to some species from temperate floodplains in Europe that spread their reproductive effort over two seasons, species of wolf spiders on the floodplain of an upland river in Victoria have a single reproductive season (Framenau 1998). Framenau

(1998) supposed that variability in flood regime dispersed throughout the whole year might provide a selective pressure against staggered reproductive effort in Australian floodplain hydrophiles. However, the opposite also could be argued. Framenau's (1998) contention ignores the marked seasonality in flood patterns in some sections of temperate Australian river-floodplain systems. For instance, before river regulation, flooding did not occur in late summer and early autumn in Barmah Forest (Bren 1988).

Thus, the fauna in sub-humid, geologically recent Barmah Forest is likely to have been characterized by traits such as high mobility and tolerance of a range of habitat conditions, which facilitate persistence in a highly variable environment. Fauna from floodplains with more regular flood patterns share many of these life-history characteristics, suggesting that habitat variability rather than unpredictability is the main selective pressure operating on hydrophiles (cf. Junk *et al.* 1989; Walker *et al.* 1995; Tockner *et al.* 2000).

The length of time that ephemeral wetland habitat is available for hydrophiles may be short in sub-humid environments, where evaporation rates are high, necessitating adaptations for rapid transition through life-history stages not seen in temperate fauna from humid regions. There do not appear to be any data on the length of reproductive periods or maturation time for hydrophiles from sub-humid regions, preventing comparisons with temperate and tropical species at this time.

Can opportunistic hydrophilic species persist in 'predictable' environments?

Reduction in flooding associated with regulation of Australian river systems is considered likely to displace natural opportunistic assemblages in favour of species adapted for seasonally stable, low-flow environments (Walker *et al.* 1995). However, there is no reason *per se* why species cannot exploit both temporarily flooded areas (unpredictable, transient habitat) and channel edges (reasonably predictable, permanent habitat). The banks of the Murray River and anastomosing creeks were sampled to determine whether the opportunistic species that exploit the flooded forest-floor habitat were able to persist in the more stable habitat around channel margins. Moira-grass wetlands also were sampled, as these temporary wetlands flood more frequently than the forest floor and, therefore, might provide refugia for hydrophilic taxa during dry periods. The results of the comparison of assemblages between microhabitats were unclear because of the small sample sizes and problems with potential temporal shifts in assemblage structure arising from not taking all samples simultaneously. Most of the flooded forest floor sites were sampled in January 2001 and the other habitats were sampled in January 2003. Temporal shifts in assemblage composition are likely to have occurred during the time between the two sampling events because invertebrate assemblages are highly dynamic (cf. Judas *et al.* 2002).

Variation in assemblage structure does not provide information about the capacity of individual species to persist in different habitat types. The IndVal test of habitat fidelity (Dufrêne and Legendre 1997) was used to assess the exclusivity of species to either temporary-wetland habitat (flooded forest floor, moira-grass wetlands) or channel-edge habitat. Only one of the three wolf-spider species trapped in high enough numbers for testing (≥ 20 specimens) showed a preference for temporary, lentic wetlands above channel edges. Given the generalized habitat requirements of many of the floodplain wolf spiders (Table 4.1), it is not surprising that some species inhabit both temporarily inundated, lentic environments and channel edges. Contrary to the predictions of Walker *et al.* (1995), some taxa appear able to exploit conditions created by both unpredictable flood events and predictable, seasonal flows.

Three of the four carabid beetles that were examined exhibited non-random distributions between temporary wetlands and channel edges. The most commonly trapped beetle along channel margins, the bombardier beetle *Pheropsophus verticalis*, was not caught in any lentic environments, although Moore (1980) asserted that it is abundant on billabong (oxbow lake) margins. Conversely, *Platycoelus prolixus* and *Catadromus lacordairei* showed high fidelity to lentic, temporarily inundated areas and thus, might be negatively affected by reduction in flooding associated with river regulation.

High mobility, necessary to exploit ephemeral habitat, also might confer a level of robustness to changes in flood regime because high mobility enables movement between remaining suitable habitats. Turin and den Boer (1988) found that fully

winged ground beetles, with high powers of dispersal, were the most successful at persisting in the increasingly disturbed and fragmented European landscape over a period of 110 yr. However, even highly mobile populations declined if suitable habitat patches become too rare or too isolated (Desender and Turin 1989). Ground beetle populations are subject to extreme fluctuations in density (e.g. den Boer 1981). Therefore, while the opportunistic characteristics of the river red gum forest hydrophiles enables species to persist despite river regulation, the available habitat, and hence, the populations of ground beetles and wolf spiders, are likely to be reduced by disruption to natural flood regimes. In turn, ecological processes that hydrophiles contribute to, including the transfer of energy across the interface between aquatic and terrestrial systems, potentially are affected adversely.

Impact of flooding on beetle and spider assemblages—short-term disturbance and long-term habitat change

Despite conditions on some Australian floodplains not being considered conducive to adaptations specific to flooding (Walker *et al.* 1995), there was an influx of hydrophilic ground beetles and wolf spiders into inundated areas (Fig. 4.5 and 4.9). This influx appears to compensate for any short-term reduction in abundance or species richness of other taxa vulnerable to flooding. Hence, total spider biomass was not different between areas that experienced extended inundation and brief or no inundation (Table 4.14), despite mean spider biomass being greatest on the least flood-prone sites (Table 4.13). The occasional presence of large, burrowing wolf spiders, in particular *Lycosa leuckartii* (Thorell), on dry sites was responsible for the high mean body mass at dry sites. On flood-prone sites, the absence of large wolf spiders was compensated for by the influx of many smaller hydrophilic wolf spiders (cf. Steggles 2001).

In contrast, beetle biomass was two orders of magnitude greater in areas that experienced prolonged flooding relative to unflooded or briefly flooded sites because of the high numbers of large ground beetles attracted to the flooded areas (Table 4.8). This biomass increase may have implications for insectivorous vertebrates, such as the yellow-footed antechinus *Antechinus flavipes* (Waterhouse). *A. flavipes* reached high

densities in a Murray-River floodplain forest following the 2000-2001 flood (Mac Nally and Horrocks 2002). The specific cause of the population irruption is unknown, but given that *A. flavipes* are voracious feeders on large beetles, a flood-associated increase in beetle biomass may be responsible (Mac Nally and Horrocks 2002).

Tracking the invertebrate assemblages for 2 yr after the 2000–2001 flood enabled the long-term impact of flooding to be assessed. In the long-term, the abundance and species richness of beetles and spiders was not affected negatively by inundation. Overall, the species richness of beetles was greatest at flood-affected sites (Table 4.5), even when hydrophilic ground beetles were no longer present (Table 4.6). Moreover, when each survey was considered separately, a gradient of increasing beetle abundance with longer flood duration was evident in spring and summer (Table 4.4). Neither the abundance nor the species richness of spiders exhibited a clear, graduated response to flooding, although there was some evidence that species richness of spiders was greater on sites subject to an intermediate duration of flooding compared to dry sites (Tables 4.9-4.12).

Flooding is often described as 'resetting' systems (e.g. Junk et al. 1989; Décamps 1993). This may be interpreted to mean that, with sufficient time since flood disturbance, the biota will converge between flood-affected and dry areas (*sensu* Ward and Tockner 2001). In the present study, assemblage structure was compared between treatments at each survey time to assess whether assemblages exhibited increasing similarity as more time elapsed since the 2000–2001 flood. Little consistent evidence for convergence was found (Table 4.15 and 4.19). Flooding creates persistent changes in habitat structure that are likely to account for many of the long term differences in beetle and spider assemblages between areas that experienced different durations of inundation. Flooding produces a denser tree canopy (Stone and Bacon 1995), reducing insolation of the ground layer. Inundation results in greater production of leaf litter (Briggs and Maher 1983; Stone and Bacon 1995), as well as higher soil-moisture levels that promote fungal and bacterial activity (Molles *et al.* 1998).

Long-term, flood-associated habit change might account for differences in the species richness of beetles and the assemblage composition of spiders before the 2000–2001 flood (Table 4.5 and 4.19), as well as explaining why the composition of beetle

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assemblages varied between sites 2 yr after flooding (Table 4.15). Two years after the 2000–2001 flood, a cryptophagid species and a laemophloeid species were among the most influential species contributing to dissimilarities in beetle-assemblage composition between sites subjected to prolonged inundation and brief or no inundation (Table 4.17). These species eat mould in leaf litter (Lawrence and Britton 1991) and their distributions probably reflect greater resource availability and productivity in flood-affected habitat. It is unclear whether flood-associated habitat changes are augmented by floodwaters recharging subterranean aquifers that subsequently supply river red gums in flood-affected areas for an extended period after floodwaters subside (Dexter 1978).

The relationship between flood-associated habitat change and long-term patterns in assemblage structure was less clear for spiders. Immediately after the 2000–2001 flood, the distribution of wolf spiders was an important determinant of assemblage dissimilarity between sites that experienced different durations of inundation (Table 4.20). Wolf spiders also were abundant on flood-affected sites in November 2001, 10 mo after the flood receded (Fig. 4.9), making it possible that seasonal factors, rather than flooding, determined the abundance of wolf spiders. Wolf spiders comprised a large proportion of the spider fauna at sites that experienced extended flooding for three consecutive sampling periods after the flood and then declined (Fig. 4.8a). This suggests that flooding was responsible for the increased numbers of wolf spiders, but that flooding made habitat suitable for wolf spiders for a longer time than for ground beetles.

Nine species of wolf spider were captured throughout the forest in January 2001 and only three species were captured in November 2002. Moreover, the composition of the wolf spider assemblages changed over the 10 mo from species that are very waterdependent to species that tolerate drier conditions. For instance, *Trochosa expolita* (Simon), a species that prefers well-watered lawns and the banks of temporary creeks (McKay 1979) was present immediately after flooding but later was succeeded by *Venatrix pseudospeciosa* Framenau and Vink and *Artoria 'victoriensis'* nov. sp. species with only moderate affinity for water (V.W. Framenau, Western Australian Museum, pers. comm.). Thus, the distributions of wolf spiders primarily are attributable to flooding, although seasonal effects have some influence. Seasonal peaks in zodariid spider activity on dry/briefly flooded sites (Fig. 4.8b) also contributed to fluctuating R-statistic values (Table 4.19), so that the spider faunae at sites subject to different durations of inundation did not appear to converge smoothly over time.

Determining the relative importance of flood disturbance *per se* and flood-associated habitat change to floodplain invertebrate assemblages is difficult because the two factors co-vary. Separation of the two factors was not attempted in the present study, although it is notable that spiders did not respond to changes in habitat structure arising from the distribution of fallen timber (Chapter Three). Various components of habitat structure are known to influence floodplain-spider assemblages, including leaf-litter densities (Uetz 1976), vegetation biomass (Bell *et al.* 1999) and vegetation structure (Bonn *et al.* 2002). Bonn *et al.* (2002) contended that spiders respond to changes in habitat structure rather than to flood regime, but the two effects largely are inseparable. Moreover, hydrophilic spiders are consistently found on very flood-prone sites (e.g. Uetz 1976; Höfer 1989; Bell *et al.* 1999; Bonn *et al.* 2002). Ground beetles widely are considered to respond primarily to moisture levels (Bonn *et al.* 2002).

The impact of flooding on other taxa also might have a direct effect on beetle and spider assemblages. Overall, the most flood-prone sites had the lowest abundance and diversity of ants (Chapter Five). Hering (1995) demonstrated that ants are superior competitors to beetles in riparian zones. Thus, the more flood-prone sites might offer reduced levels of competition and predation to beetles. However, ants were trapped in considerably greater numbers than beetles at all sites (Chapter Five). Moreover, the magnitude of the difference in the species richness of ants and beetles between sites was small and the overall biological significance of the finding is unclear (Fig. 4.3). Similarly, zodariid spiders, specialist predators of ants, were consistently more abundant on drier sites (Chapter Five).

Implications for the Flood Pulse Concept

Junk et al. (1989) contended that the unpredictable flood pulses "impede the adaptation of organisms and are counterproductive for many of them." The present study revealed

that hydrophiles in an area subjected to unpredictable flooding share many charac cristics with the fauna from unregulated floodplains in temperate regions. Moreover, these characteristics are likely to be adaptations to environmental variability rather than to unpredictability. In the short-term, flooding boosts the productivity of sub-humid floodplain forest, supporting a temporary pulse in biomass of predatory hydrophiles. In the longer term, flooding was not "counterproductive" to beetle or spider diversity.

The imprint on habitat created by different local flood regimes is just as important to maintenance of biodiversity as the flood perturbation because, although more subtle, the effects of habitat structure on invertebrate assemblages probably last for years. Moreover, the persistent influence of flood-associated habitat change is consistent with the FPC (Junk *et al.* 1989). Thus, the response of biota in a regulated river-floodplain system to managed inundation can be understood in terms of a flood pulse model.

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Table 4.1. Historic distribution records and natural history information on hydrophilic ground beetles and wolf spiders in river red gum forest. The number in brackets denotes the total number of specimens collected in pitfall traps during the study.

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Ground beetle species caught on the forest floor after extended flooding	Known distribution from literature	Notes
Platycoelus prolixus (Er.) (Pterostichinae) (237)	Australia (universal) including Tasmania ((Sloane 1903) as <i>Chaenioidius prolixus</i>)	This species is apparently a mixture of several undescribed, related taxa (M. Baehr, Zoologische Staatssammlung Münchhausenstraße pers. comm.)
Catadromus lacordairei Bois. (Pterostichinae) (34)	Generally distributed in Australia, including Tasmania (Sloane 1920) (Moore 1965; Littlejohn and Wainer 1978); very common along the Murray River(Moore 1980).	
Pseudoceneus sol(l)icitus (Er.) (Pterostichinae) (79)	Tasmania (Sloane 1920)	
Tachys sp. 7 (Bernbidiinae) (4)	?	Probably a new species (M. Baehr, Zoologische Staatssammlung Münchhausenstraße pers. comm.)
Dicrochile quadricollis Cast. (Licininae) (7)	Flinders Island, Victoria (Sloane 1920)	
Microlestodes macleayi (Cs.) (Licininae) (5)*	South Australia, statewide (Matthews 1980) Microlestodes are mesophilous beetles of open forest country to mountain forests. Very little known on the habits of nearly all species (Baehr 1987).	Bachr (1987) erected a new genus Microlestodes for all Australian species previously placed in Microlestes. *Confused with M. australiensis (SI.) in samples

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	Murray River (Moore 1980).	
	of billabongs, and is abundant along the	
	occurs in damp places, especially the margins	
	wet places (Matthews 1980). This species	(Brachininae) (42)
	Widespread in eastern Australia occurring in	Pheropsophus verticalis Dej.
		channel edges
		Ground beetle species caught on
	to central Queensland (Framenau 2002)	
	Tasmania (?) (Sloane 1903); castern Victoria	(Pterostichinae) (45)
	Common on the Murray River, also	Loxandrus subiridescens (Macl.)
		(Pterostichinae) (Chd.) (22)*
	ذ	Rhytisternus laevilaterus
	and Edward 1998)	
	on agricultural land in the present day (Horne	
	mainland, Tasmania (Sloane 1920); common	(Pterostichinae) (22)*
*Confused with R. laevilaterus in samples	Common and widespread on Australian	Rhytisternus liopleurus (Chd.)
		(Harpalinae) (8)
	i	Lecanomerus discoidalis (Blackb.)
	(Sloane 1896)	
	being helped by the Murray river-system	
	that its range is evidence for its distribution	(Scaritinae) (8)
2	Recorded on the Murray by Sloane who notes	Cliving quadratifrons Sl.
		(Licininae) (5)
	See comment above	Microlestodes australiensis (SI.)
		2010001
		the forest floor after extended
Notes Notes	Known distribution from literature	Ground beetle species caught on

Table 4.1. continued

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Table 4.1. continued

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Wolf spider species caught on the forest floor after extended flooding	Known distribution from literature	Notes
Lycosa nr. alteripa (11)	?	Probably an undescribed species (V.W.Framenau, Western Australian Museum pers. comm.)
Venatrix pseudospeciosa Framenau and Vink (173)	The most common wolf spider in suburban gardens in South Australia and Victoria, also south New South Wales and Tasmania (Framenau 2001)	
Artoria 'victoriensis' nov.sp. (92) Framenau, Gotch & Austin (manuscript in prep.)	The species is very common in Victoria and South Australia, but also into southern NSW and the ACT. It inhabits moderately moist areas, normally shaded, and is quite common in suburban Melbourne and Adelaide (V.W.Framenau, Western Australian Museum pers. comm.)	
Trochosa expolita (Simon) (100)	Abundant on well-watered lawns and pastures, also banks of temporary creeks, Western Australia and South Australia (McKay 1979)	McKay (1979) considers the western Australian specimens to be a different "subspecies" to the eastern Australia specimens, but the specimens collected in this study clearly had the morphological characteristics of the western "subspecies."
Hogna tongatabuensis (Strand) (17)	Widespread in Australia near water; also New Zealand and some Pacific islands (V.W.Framenau, Western Australian Museum pers. comm.)	Possible synonym with Lycosa crispipes L.Koch; also synonymous with Lycosa waitei (Rainbow).

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Table 4.2. Comparison of C	Clivina (Carabidae;	Scaritinae) s	pecies trapped	in the	Riverina b	y Sloane	(1896)	with speci	es trapped	l in the
current study.										

Clivina species	Riverina District (Sloane 1896)	Current Study	Notes
C.australasiae Bohemann	/	√*	
C.basalis Chaudoir C.biplagiata Putzeys		√	
C.felix Sloane	✓	✓	Some uncertainty about whether C. felix is a separate species from C. basalis (M. Baehr, Zoologische Staatssammlung Münchhausanstreße new gemm.)
C.heterogena Putzeys		√*	Muncimausenstrabe pers. comm.)

SƏDON	MOWB GISTFIDUIOG ITOM REFERENCE	wen spider species caught on the forest floor after extended flooding
	Currently known from Victoria and South	Artoria howquaensis Framenau
	Australia (Framenau 2002). Banks of lowland	(23)
	sames in the Great Artesian Basin in South	
	Australia (Travis Gotch, pers. comm.).	
	Open areas near water, Australia (widespread)	Venatrix goyderi (Hickman) (2)
	and New Zealand (Framenau 2002)	
		study with a historical Species not caught in the current
		ofistribution suggesting they
	Very common along the Murray River (Moore)	Catadromus australis (Cast. (0):
	Rate along the Murray River and much rater than C-lacordairer in general (M. Bachr, Zoologische Staatssammlung	
	Munchhausenstraße pers.comm.) Introduced to Australia from South America	Bembidion brullei (Gemminger and
	some mine between 1924 and 1924. Widespread in Murray-Darling Basin (Moore -	

Table 4.1. continued



* Denotes species that M.Baehr will check against types to confirm identifications in February 2004.

deemed to be a substantial change.	* ≥ 0.90 or ≤ 0.10 for negative differences,
	" ln(x + 1) transformed

^z g-£g	Extended flooding – moderate flooding	81.0 ± £1.0	-0.22, 0.49	62.0
IG-€G	Extended flooding – brief/no flooding	61.0 ∓ I2.0	19.0 ,41.0-	88.0
<i>\d-zd</i>	Moderate flooding – brief/no flooding	01.0 ± 80.0	05.0,85.0-	69.0
٤d	Solicient for extended flooding	21.0 ± 06.2	5.65, 3.14	*0.1
zd	Coefficient for medium flooding	41.0 ± 97.2	2.48, 3.07	*0°1
١ď	Coefficient for brief/no flooding	21.0 ± 69.2	2:36, 2.97	*0.1
ø	Coefficient for autumn/winter sampling	81.0 ± 10.0	67.1 '85'0	*0'1
Parameter	Description	Mean`± SD	95% credible interval	Posterior probability mass

Table 4.3. Critical parameter details for the Bayesian analysis of total beetle abundance[#].

Table 4.4. Bayesian analysis of mean differences in total beetle abundance[#] between flood treatments at each survey time.

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
μσγι	Mean differences in abundance between flood treatments May 2000 (8 mo before flood)	-0.12 ± 0.17	-0.44, 0.26	0.23
μ _{ðY2}	Mean differences in abundance between flood treatments January 2001 (immediately after flood)	-0.54 ± 0.46	-1.21, 0.04	0.05*
μ _{δY3}	Mean differences in abundance between flood treatments May 2001 (4 mo after flood)	0.27 ± 0.53	-0.38, 1.04	0.51
µsr4	Mean differences in abundance between flood treatments November 2001 (10 mo after flood)	$\textbf{-0.20} \pm 0.13$	-0.45, 0.07	0.08*
μərs	Mean differences in abundance between flood treatments January 2002 (12 mo after flood)	-0.21 ± 0.13	-0.44, 0.07	0.07*
μετε	Mean differences in abundance between flood treatments November 2002 (22 mo after flood)	-0.20 ± 0.13	-0.43, 0.08	0.08*
μ _{δΥ7}	Mean differences in abundance between flood treatments January 2003 (24 mo after flood)	-0.17 ± 0.13	-0.44, 0.10	0.09*

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[#] $\ln(x + 1)$ transformed * ≥ 0.90 or ≤ 0.10 for negative differences * ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

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) be a substantial change.	differences, deemed t	svitegative for negative ≥ 0.10 for negative

^z g-£g	guibooft ətsrəbom – guibooft bəbnətxÄ	60.0 ± 02.0	0.02, 0.39	*86.0
'g-tg	Extended flooding – brief/no flooding	01.0 ± 15.0	0.12, 0.50	*0.1
'd-zd	Moderate flooding – brief/no flooding	11.0 ± 11.0	26.0,01.0-	۲8.0
٤J	Coefficient for extended flooding	70.0 ± 10.2	1,88, 2,13	*0°1
zg	Coefficient for medium flooding	80.0 ± 18.1	96'1 '99'1	*0°1
'g'	Coefficient for brief/no flooding	80.0 ± 07.1	98.1 ,42,1	*0°1
ø	Coefficient for autumn/winter sampling	80.0 ± 70.0-	60,0 ,62,0-	07:0
Parameter	Description	dS ± ns∋M	95% credible interval	Posterior probability mass

Table 4.5. Critical parameter details for the Bayesian analysis of species richness of total beetles.

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Table 4.6. Bayesian analysis of mean differences in species richness of total beetles between flood treatments at each survey time.

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
μ _{δΥ1}	Mean differences in abundance between flood treatments May 2000 (8 mo before flood)	-1.17 ± 0.47	-2.11, -0.25	0.01*
<i>µб</i> ү2	Mean differences in abundance between flood treatments January 2001 (immediately after flood)	-1.77 ± 0.53	-2.96, -0.80	0*
μ _{δY3}	Mean differences in abundance between flood treatments May 2001 (4 mo after flood)	-1.01 ± 0.49	-1.92, 0.08	0.03*
µ574	Mean differences in abundance between flood treatments November 2001 (10 mo after flood)	-1.53 ± 0.50	-2.58, -0.60	0*
µsys	Mean differences in abundance between flood treatments January 2002 (12 mo after flood)	-1.33 ± 0.44	-2.20, -0.46	0*
μ _{δγ6}	Mean differences in abundance between flood treatments November 2002 (22 mo after flood)	-1.11 ± 0.48	-2.00, -0.11	0.02*
μ817	Mean differences in abundance between flood treatments January (24 mo after flood)	-1.45 ± 0.45	-2.36, -0.59	0*

Parameter	Description	Mean \pm SD	95% credible interval	Posterior probability mass
βι	Coefficient for brief/no flooding	1.18±0.51	0.08, 2.13	0.98*
β_2	Coefficient for medium flooding	1.77±0.47	0.74, 2.68	1.0*
β_3	Coefficient for extended flooding	4.26±0.44	3.37, 5.02	1.0*

Table 4.7. Critical parameter details for the Bayesian analysis of variation in mean mass of beetles across sites subject to different durations of flooding, January 2001[#].

Table 4.8. Critical parameter details for the Bayesian analysis of variation in total biomass of beetles across sites subject to different

*Data natura	bernolsnert gol i		•	
zd-ed	Extended flooding – moderate flooding	47.0 ± 89.£	5.26, 5.21	*0.1
\G-&G	Extended flooding – brief/no flooding	9L'0 T 97'7	5'94' 2'61	*0.1
ıg₋īg	Moderate flooding brief/no flooding	\$8.0±77.0	-1:02, 2,20	68.0
¢ g /	Coefficient for extended flooding	8.0±0.50	86.8 ,60.7	*0'1
īd,	Coefficient for medium flooding	4.32±0.56	25.2 ,71.5	*0'1
'g'	Coefficient for brief/no flooding	09° F\$\$*E	2.37, 4.82	*0.1
Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

durations of flooding, January 2001[#].

$\beta_2 - \beta_1$	Moderate flooding – brief/no flooding	0.65 ± 0.72	-0.79, 2.08	0.04
β_3 - β_1	Extended flooding - brief/no flooding	3.15 ± 0.62	1.82, 4.37	1.0*
β_3 - β_2	Extended flooding - moderate flooding	2.50±0.04	1.22, 3.67	1.0*

[#]Data natural log transformed

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
μ _{δγι}	Mean differences in abundance between flood treatments May 2000 (8 mo before flood)	0.22 ± 0.25	-0.12, 0.72	0.82
$\mu_{\delta Y2}$	Mean differences in abundance between flood treatments January 2001 (immediately after flood)	-0.07 ± 0.12	-0.24, 0.16	0.33
Ц _{бҮЗ}	Mean differences in abundance between flood treatments May 2001 (4 mo after flood)	0.22 ± 0.23	-0.11, 0.56	0.81
11 ₈₇₄	Mean differences in abundance between flood treatments November 2001 (10 mo after flood)	-0.08 ± 0.13	-0.27, 0.15	0.32
U _{SYS}	Mean differences in abundance between flood treatments January 2002 (12 mo after flood)	-0.05 ± 0.10	-0.20, 0.16	0.33
4876	Mean differences in abundance between flood treatments November 2002 (22 mo after flood)	-0.03 ± 0.10	-0.20 - 0.17	0.36
45877	Mean differences in abundance between flood treatments January 2003 (24 mo after flood)	-0.10 ± 0.15	-0.36, 0.16	0.30

Table 4.10. Bayesian analysis of mean differences in total spider abundance[#] between flood treatments at each survey time.

₹ J -£J	Extended flooding – moderate flooding	11.0 ± 11.0-	-0.33, 0.12	<u> </u>
'g-&g	Extended flooding – brief/no flooding	21.0 ± 20.0-	12.0 ,72.0-	18.0
<i>\</i> g- <i>z</i> g	Moderate flooding – brief/no flooding	21.0 ∓ 90.0 [°]	££.0 ,61.0-	69.0
ŕg	Coefficient for extended flooding	2.72 ± 0.08	2:26, 2.87	*0°I
^z d	Coefficient for medium flooding	2.83 ± 0.09	20.5 ,202	*0`I
'\$	Coefficient for brief/no flooding	60 [.] 0 ± 97.2	2.56, 2.93	*0.1
ø	Coefficient for autumn/winter sampling	11.0 ± 70.1-	-1.28, -0.84	*0
Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass

Table 4.9. Critical parameter details for the Bayesian analysis of total spider abundance[#].

bernolzner) (I + x)nf[#]

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

[#] in(x +1) transformed

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≥ 10 09.0≤ *	o.10 for negative differences, deemed to b	leitnetedue e s	ະອາຊາດ	
zg-sg	Extended flooding – moderate flooding	80.0 ± 60.0-	-0.24, 0.08	0.14
'g-&g	Extended flooding – brief/no flooding	60.0 ± 20.0	-0.14, 0.19	09.0
Ig-zg	Moderate flooding – brief/no flooding	60.0 ± 11.0	-0.06, 0.28	*06'0
٤J	Coefficient for extended flooding	90'0∓96'1	80.2 ,28.1	*0,1
zg	Coefficient for medium flooding	2.05 ± 0.06	1.5, 501	*0.1
'g	Coefficient for brief/no flooding	70.0 ± 46.1	181, 2.06	*0'1
Ø	Coefficient for autumn/winter sampling	01.0 ± 68.0-	02.0- ,60.1-	*0
Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass

Table 4.11. Critical parameter details for the Bayesian analysis of species richness of total spiders.

Table 4.12. Bayesian analysis of mean differences in species richness of total spiders between flood treatments at each survey time.

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
μσγι	Mean differences in abundance between flood treatments May 2000 (8 mo before flood)	-0.03 ± 0.17	-0.37, 0.30	0.43
μ _{δY2}	Mean differences in abundance between flood treatments January 2001 (immediately after flood)	-0.09 ± 0.40	-0.85, 0.76	0.41
<i>µ5</i> үз	Mean differences in abundance between flood treatments May 2001 (4 mo after flood)	-0.01 ± 0.17	-0.34, 0.34	0.46
μσγι	Mean differences in abundance between flood treatments November 2001 (10 mo after flood)	-0.13 ± 0.41	-0.94, 0.66	0.37
Hors	Mean differences in abundance between flood treatments January 2002 (12 mo after flood)	-0.11 ± 0.40	-0.88, 0.67	0.39
Цвуб	Mean differences in abundance between flood treatments November 2002 (22 mo after flood)	-0.11 ± 0.41	-0.89, 0.70	0.40
µ877	Mean differences in abundance between flood treatments January 2003 (24 mo after flood)	-0.14 ± 0.40	-0.93, 0.67	0.37

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

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Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
βι	Coefficient for brief/no flooding	2.79±0.22	2.38, 3.25	1.0*
β_2	Coefficient for medium flooding	1.92±0.20	1.51, 2.33	1.0*
β_3	Coefficient for extended flooding	2.26±0.19	1.89, 2.62	1.0*
<u> </u>		0.0010.01	1.60 0.21	^ *

Table 4.13. Critical parameter details for the Bayesian analysis of variation in mean mass of spiders across sites subject to different durations of flooding, January 2001#.

Table 4.14. Critical parameter details for the Bayesian analysis of variation in total biomass of spiders across sites subject to different

			hamolanent pol le	miten etea #
*/6'0	-0.04, 1.52	07,0±47.0	Extended flooding – moderate flooding	zd-ed
0:30	65.0 ,61.1-	-0.24±0.44	Extended flooding – brief/no flooding	<i>\g-\g</i>
*10'0	≠l'0- ' 96'l-	<i>⊾</i> ₽.0±70.0-	Moderate flooding – brief/no flooding	<i>\G-t</i> G
*0°I	4.52, 5.60	82.0 1 70.2	Coefficient for extended flooding	ŕď
*0.1	£6 [.] 4 ,68.£	15.0±45.4	Coefficient for medium flooding	ζg
*0.1	10'9 '02'+	45.0±15.2	Coefficient for brief/no flooding	'g'
Posterior probability mass	95% credible interval	Mean ± SD	Description	Parameter

DOULLOISURIN SOL IRINNEL RIBGI

durations of flooding, January 2001[#].

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

$p_2 p_1$	inducate neocang one neocang			
β3-β _l	Extended flooding – brief/no flooding	-0.53±0.29	-1.10, 0.02	0.03*
β_3 - β_2	Extended flooding – moderate flooding	0.33±0.27	-0.17, 0.88	0.90*

[#]Data natural log transformed

Table 4.15.	Analysis	s of similarit	ies results for beetle	assemblages	sampled before a	and over a	1 2-yr period	after flooding i	n 2000–2001
(excludes si	tes that re	e-flooded in 2	2002–2003).						
Sampling time	Months since	Total beetles trapped to	Extended flooding vs. by flooding	rief/no Mo floo	derate flooding vs. b	rief/no	Extended flo flooding	ooding vs. moderate	

R

0.056

P-value

0.271

Permutations

462

flood

Pre-

May 2000

characterize assemblage

322

•

R

0.160

P-

value

0.087

Table 4.16. Beetles contributing most to dissimilarity in assemblages between sites that experienced extended and brief/no flooding,

Catadromus lacordairei Bois. (Catabidae)	2.2	0	6.0	8.4	
Pseudoceneus sollicitus (Er.) (Carabidae)	2.2	0	0.1	0.6	
Brachypeplus sp. (Nitidulidae)	0.0	٤.1	8.1	0.01	
Platycoelus prolixus (Et.) (Carabidae)	0.12	0	61	50.1	
	Extended flooding	Brief flooding	Average Dissimilarity/ SD	% Dissimilarit	
	oonsbauds ogstovA				

January 2001.

P-

value

0.918

Permutations

462

R

-0.168

	flood	(16 sites)									
January 2001	0	626	0.735	< 0.001	11 440	0.153	0.038	6435	0.480	< 0.001	20 000
May 2001	4	3164	0.213	0.035	11 440	0.082	0.110	6435	0.016	0.321	20 000
November	10	763	0.215	0.014	11 440	0.084	0.143	6435	0.110	0.098	20 000
2001						l					
January	12	323	0.106	0.131	11 440	0.197	0.018	6435	-0.034	0.664	20 000
2002											
November	22	564	0.136	0.069	6435	0.304	0.006	1716	0	0.481	3003
2002	1	(21 sites)	1								
January	24	313	0.373	< 0.001	6435	-0.079	0.682	792	0.143	0.136	1287
2003		(20 sites)									

Permutations

126

.

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Table 4.18. ANOSIM results for comparison of flooded forest-floor beetles assemblages 2001 v	with fauna from sites that were re-flooded in
2003 and with moira-grass wetlands (MGW) and channel-edge (CE) sites 2003.	

11 440

Comparison	R	P-value	Permutations
Extended flooding forest floor 2001 vs. re-flooding forest floor 2003	0.937	0.001	715
Moderate flooding forest floor 2001 vs. re-flooding forest floor 2003	0.464	0.008	495
Brief/no flooding forest floor 2001 vs. re-flooding forest floor 2003	0.177	0.13	330

Table 4.17. Beetles contributing most to dissimilarity in assemblages between sites that experienced extended and brief flooding, January

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2003.

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Species 8C (Staphylinidae)	£.1	٤.٢	9.0	9.6					
Cryptolestes sp. (Laemophlocidae)	2.1	0.1	0.1	1.01					
(?)Agrypnus sp. (Elateridae)	0	L'E	8.0	9.61					
Species 14 ((?)Cryptophagidae)	9'1	£.0	8.0	14.8					
-	Extended flooding	Brief flooding	Average Dissimilarity/ SD	% Dissimilarity					
	Average abunda	Average adundance							

	••••	
Extended flooding forest floor 2001 vs. MGW 2003	0.793	0.018
Moderate flooding forest floor 2001 vs. MGW 2003	0.481	0.089
Brief/no flooding forest floor 2001 vs. MGW 2003	0.360	0.083
Re-flooding forest floor 2003 vs. MGW 2003	0.964	0.067
Extended flooding forest floor 2001 vs. CE 2003	0.806	< 0.001
Moderate flooding forest floor 2001 vs. CE 2003	0.567	0.001
Brief/no flooding forest floor 2001 vs. CE 2003	0.417	0.002
Re-flooding forest floor 2003 vs. CE 2003	0.612	0.003
	,	

	Extended flooding	Brief flooding	Average Dissimilarity/ SD	% Dissimilarity
Trochosa expolita (Simon)	7.3		1.3	12.3
(Lycosidae)		·		
Neostorena sp. nov. (Zodariidae)	0	3.9	1.1	9.3
Habronestes raveni Baehr (Zodariidae)	0	1.9	1.2	7.0
Artoria 'victoriensis' nov. sp.	3.0	0.7	0.9	6.7
Framenau, Gotch & Austin (mauscript				
name) (Lycosidae)				
Hogna tongatabuensis (Strand)	14	0	11	57
(Lycosidae)	•••	U U	***	5.7
Artoria howguaensis Framenau	3.0	0.1	0.7	5.3
(Lycosidae)				

Average Abundance

2001.

(excludes sites that re-flooded in 2002-2003).

Table 4.20. Spiders contributing most to dissimilarity in assemblages between sites that experienced extended and brief flooding, January

Table 4.19. Analyzes of simuarities results for spider assemblages sampled before and over a 2-yr period after flooding in 2000-2001

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			co0:0	771			6010	C10:0	0.0710	(20 sites)	17	5003
	2801	1760	£90 0	C6L	£6C U	250.0	5279	0100	9860	606 (Saus 17)	70	7007
	2002	661.0	Z80 ⁻ 0	91/1	270.0	191.0	\$543	٢٥٥.0	£\$£.0	403 403	52	November
												2002
ļ	20 000	001.0	<i>L</i> 60°0	5549	900'Ò	0.330	074 []	100.0 >	¢7ð.0	909	15	January J
]					1002
	20 000	620.0	601.0	56435	200.0	725.0	11 440	100.0 >	202.0	9 <i>L</i> †	01	November
	20 000	0.428	200.0	6432	6.053	091.0	11 440	700.0	692.0	174	4	1002 YeM
												1007
	20 000	100.0	104.0	56435	900.0	125.0	11 440	100.0 >	817.0	698	0	January
										(5015-01)		
	 .							-		(16 sites)	pooli	and the
	971	0.444	£10.0	971	2910	051.0	971	50.0	515.0	28	Pre-	0002 vem
l	CHANGED DE LA I		17	SHORING IN IN I	auley	17	SHOUPDOULD I	- T	17	!	{ :	
	2nniteterrag	auley-Q	<u> </u>	Permitetumred	<u></u>	<u>a</u>	Period	d	<u> </u>	agniauuacen		
										aveldmasse	00011	
	moderate Hooding			DUGUAD HOODING			DIJEL/NO HOOGING			or bound to	- poolt	
	Extended hooding vs.			INTODERAIC INOOTING VS.			EXICUTED IIOODIR VS.			t puper to	SUBUOIA	gunquisc
ł	sv prihooft hahratyA			ou puibooft etershold			Principooli behastri			mehina letoT	2410014	nailame2
Table 4.22. A	nalysis of similarities re	sults for comparise	on of flooded fo	prest-floor spider	assemblages	2001 with	fauna fron	sites t	hat were			
---------------	----------------------------	---------------------	------------------	--------------------	-------------	-----------	------------	---------	----------			
re-flooded in	2003 and with moira-gra	ass wetlands (MGV	V) and channel-	edge (CE) sites 2	.003.							

Comparison	R	<i>P</i> -value	Permutations
Extended flooding forest floor 2001 vs. re-flooding forest floor 2003	0.608	0.001	715
Moderate flooding forest floor 2001 vs. re-flooding forest floor 2003	0.087	0.269	495
Brief/no flooding forest floor 2001 vs. re-flooding forest floor 2003	0.529	0.003	330
Extended flooding forest floor 2001 vs. MGW 2003	0.264	0.127	55
Moderate flooding forest floor 2001 vs. MGW 2003	0.746	0.022	45
Brief/no flooding forest floor 2001 vs. MGW 2003	0.834	0.028	36
Re-flooding forest floor 2003 vs. MGW 2003	0.661	0.067	15
Extended flooding forest floor 2001 vs. CE 2003	0.432	< 0.001	11 440
Moderate flooding forest floor 2001 vs. CE 2003	0.118	0.113	6435
Brief/no flooding forest floor 2001 vs. CE 2003	0.668	0.001	1716
Re-flooding forest floor 2003 vs. CE 2003	0.124	0.212	330

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8.0

Table 4.21. Spiders contributing most to dissimilarity in assemblages between sites that experienced extended and brief flooding, January

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0.0 (asbirite Codariidae) 0.6 ĽL 0.1 0.1 (sebineboZ) suppol 0.6 8.0 1.5 Pentasteron intermedium Bacht and 0.7 (nanuscript name) (Soridae) 9.1 8.1 ٤.21 4.2 Argocienus' samueli' Raven <u>SD</u> Viralimizzid Dissimilarity/ gnibooft Average Britef flooding səicəqZ bsbnstad % ээпвbruds эрглэүА · .2003.

9.0

0

1.0

4.1

(SebiqilottevO). (Cyatholipidae)

Prodidomidae sp.

		J other taxa recorded at 1 site and not elsewhere			i other taxa recorded at l site not elsewhere			z otner taxa recorded at 1 site and not elsewhere	
	(100.0>) (<0.001)								
verticalis Dej.	cpsuvel								
darlingensis Cast. Pheropsophus	0) %12	0	0	0	0	0	1.5 ± 5.2	ç	
(Macl.) Chilaenuis		0	0	ţ	2,0 ± 2.0	ì	0		
suəəsəpiridus						,			
Blackb.) (Blackb.)		0.2 ± 0.2	I	1	0	0	1.0 ± 1.0	1	
qizcoiqajiz Jencauouvernz		£.0±4.0	z		0	0	0		
Glivina Clivina guadratifrans SL		1.0 ± 2.0	2	I	0	0	9.0 ± 9.0	I	
Dicrochile Dicrochile		1.0 ± 2.0	z	4	0	0	0		
אואנובנפרוענים (ראל)) אואנובנפרוענים געואנובנפרוענים		4.0 ± 8.0	4	4	$0 \pm i$	2	1.0 ± 1.0	I	
Microlestodes	(50:0)	2.0 ± ₽.0	4	0	0	0	0		
Catadromus Someruus (ET.)	(20 0) %85 (80 0)	£.1 ± 2.2	S	9	5.5 ± 2.5	ı	0		
Pseudoceneus (Er.)	(1000) (1000)	9.2 ± 2.8	L	£I	0	0	2.0 ± E.O	2	
Platycoelus prolixus	%£8	9'9∓0'lZ	8	30	5°1 ∓ 5°1	I	Ő		
	prackets)*		2001 (9 sites)		2003	2003 (2 sites)		····	
	ni	1002 sətiz	recorded	(siie I)	setie brisleseng	recorded	2003	(sətiz 7) £002	
	Sular-9)	forest-floor	sites where	site 2003	moira	mµete Breese	channel sites	recorded	
	measure	L) and an the second se	forest-floor	forest-floor	z) consumers	setis bnelszerg	SE) at	where	
saisada	isnosci Gdality	T Ponchaude	flooded iverage	is someonor. Percent	T and and a second s	IO ISOURNI	4) apreparde	o isonoci oi channel sites	
/0	7 - 7 - 1 - 1 - 1 - 1					The second second of the second secon	*****	1 A 1 A 1 A 1 A 1 A 1 A 1 A 1 A 1 A 1 A	

*Probability of a non-random distribution between habitat types.

Table 4.23. Relative abundance of hydrophilic ground beetles in different microhabitats and habitat-fidelity scores.

Species	Habitat fidelity measure (P-value in brackets)*	Mean abundance (± SE) at flooded forest-floor sites 2001	Number of flooded forest-floor sites where recorded 2001 (9 sites)	Abundance at flooded forest-floor site 2003 (1 site)	Mean abundance (± SE) at flooded moira grassland sites 2003	Number of moira grassland sites where recorded 2003 (2 sites)	Mean abundance (± SE) at channel sites 2003	Number of channel sites where recorded 2003 (7 sites)	Mean abundance (± S.E.) at forest-floor sites 2002 (no flooding)	Number of forest- floor site where recorded 2002 (9 sites)
<i>Venatrix pseudospeciosa</i> Framenau and Vink		0.3±0.3	1	1	1.5 ± 0.5	2	0.9 ± 0.3	4	1.3 ± 0.4	7
Trochosa expolita (Simon)	74% (0.04)	7.3 ± 2.9	7	5	3.0 ± 1.0	2	0.9 ± 0.5	3	0	0
Artoria 'victoriensis' nov. sp. Framenau, Gotch and Austin (manuscript name)	45% (0.73)	3.0 ± 1.7	7	0	0	0	1.9±0.3	7	0.8 ± 0.4	4
Hogna tongatabuensis (Strand)		1.4 ± 0.5	5	0	0	0	0	0	0	0
<i>Lycosa</i> sp. nov. (nr. <i>L. alteripa</i>)		1.0 ± 0.5	4	1	0	0	0	0	0	0
Artoriu howquaensis Framenau	47% (0.19)	3.0 ± 2.2	3	2	9.0 ± 8.0	2	0.3 ± 0.2	2	0	0
<i>Venatrix goyderi</i> (Hickman)		0.1 ± 0.1	1	0	0	0	0.1 ± 0.1	1	0	0
Aulonia sp. (undescribed)		0	0	1	0	0	0.1 ± 0.1	1	0.1 ± 0.1	1
Allocosa palabunda (Koch)		0	0	0	0	0	0.1 ± 0.1	1	0	0
Lycosa leuckarti (Thorell)		0	0	0	0	0	0.1 ± 0.1	1	0	0

Table 4.24. Relative abundance of hydrophilic wolf spiders in different microhabitats and habitat-fidelity scores.

*Probability of a non-random distribution between habitat types.

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Not flooded or flooded briefly during springsummer 2000-2001



Transition without a state change

- Moderate flooding during spring-summer 2000-2001

- Extended flooding during spring-summer 2000-2001
- Flooded during spring-summer 2002-2003

Figure 4.1. Schematic of the flooding at the 24 study sites over the survey period.

Transition with a state change



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different durations and frequency of inundation.

Figure 4.3. Mean species richness (\pm SE) of ground-active beetles over time at sites subject to

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Figure 4.5. Mean abundance (± SE) of ground beetles (Carabidae) over time at sites subject to different durations and frequency of inundation (log-linear scale).











May 2000 data not represented for extended flooding sites because only seven spiders were trapped and this was not considered a large enough sample to be representative of the fauna. Thirty-eight spiders were trapped on the briefly flooded/unflooded sites during the same survey.



Figure 4.8. Percentage of spider assemblages comprised by major families on sites that experienced (a) extended flooding in 2000-2001; (b) brief or no flooding in 2000-2001.



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Figure 4.9. Mean abundance (\pm SE) of wolf spiders (Lycosidae) over time at sites subject to different durations and frequency of inundation.

Append	ix 4.1. List of	species of Cole	eoptera captured in	Barmah Forest, M	lay 2000-
January	2003. (Ref. no	. refers to a refe	erence number used	to identify morpho	species in
the you	cher collection.))			
Ref no.	Family	Subfamily	Genus/Species	Habitat other than	Singletor
				forest floor (All	
				species listed were	
				caught in pitfall	
				traps unless stated)	
103	Anobiidae	Dorcatominae	Dorcatoma sp.	· · · · · · · · · · · · · · · · · · ·	÷
172	Anobiidae	Dorcatominae	Dorcatoma sp.		
93	Anobiidae	Dryophilinae	Dryophilodes sp.		
104	Anobiidae	Dryophilinae	Dryophilodes sp.		
183	Anobiidae	Dryophilinae	Dryophilodes sp.		
130	Anthicidae	Anthicinae	Anthicus sp.		
26	Anthicidae	Anthicinae	Formicomus sp.		
79	Anthicidae	Anthicinae	Formicomus sp.		
111	Anthicidae	Anthicinae	Formicomus sp.		
126	Anthicidae	Anthicinae	(?)Formicomus sp.		
40	Anthicidae	Anthicidae	Tomoderus sp.		
40B	Anthicidae	Anthicidae	Tomoderus sp.		
133	Anthicidae			Skirt traps.	
109	Bostrichidae	Bostrichinae	Xylion sp.		
211	Bostrichidae	Bostrichinae	Xylotillus lini		
			Blackburn		,
36	Bothrideridae		Aeschyntelus sp.		~
96	Brentidae		Cordus sp.		,
191 1	Brentidae		(?)Cyphagogus sp.	Not pitfail trapped; in skirt traps only	~
94	Buprestidae	(?)Agrilinae	?	• .	
6	Byrrhidae		Microchaetes sp.		
52	Carabidae	Agoninae	Notagonum submetallicum		
			(White)		
121	Carabidae	Apotominae	Apotomus australis		
			Castelnau		
23	Carabidae	Bembidiinae	(?)Tachys sp.		

Append	lix 4.1. List of	species of Cole	optera captured in	Barmah Forest, M	ay 2000-
January	2003. (Ref. no.	refers to a refe	rence number used	to identify morphos	species in
the vou	cher collection.)				
Ref no.	Family	Subfamily	Genus/Species	Habitat other than forest floor (All species listed were caught in pitfall traps unless stated)	Singleto
103	Anobiidae	Dorcatominae	Dorcatoma sp.	· · · · · · · · · · · · · · · · · · ·	
. 172	Anobiidae	Dorcatominae	Dorcatoma sp.		
93	Anobiidae	Dryophilinae	Dryophilodes sp.		
104	Anobiidae	Dryophilinae	Dryophilodes sp.		
183	Anobiidae	Dryophilinae	Dryophilodes sp.		
130	Anthicidae	Anthicinae	Anthicus sp.		
26	Anthicidae	Anthicinae	Formicomus sp.		
79	Anthicidae	Anthicinae	Formicomus sp.		
111	Anthicidae	Anthicinae	Formicomus sp.		
126	Anthicidae	Anthicinae	(?)Formicomus sp.		
40	Anthicidae	Anthicidae	Tomoderus sp.		
40B	Anthicidae	Anthicidae	Tomoderus sp.		
133	Anthicidae			Skirt traps.	
109	Bostrichidae	Bostrichinae	Xylion sp.	-	
211	Bostrichidae	Bostrichinae	Xylotillus lini Blackburn		
36	Bothrideridae		Aeschyntelus sp.		1
96	Brentidae		Cordus sp.		
191	Brentidae		(?)Cyphagogus sp.	Not pitfall trapped; in skirt traps only	1
94	Buprestidae	(?)Agrilinae	?	· .	
6	Byrrhidae		Microchaetes sp.		
52	Carabidae	Agoninae	Notagonum submetallicum		
	A	A	(White)		
121	Carabidae	Apotominae	Apotomus australis Castelnau		
23	Carabidae	Bembidiinae	(?)Tachys sp.		

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Append	ix 4.1. continu	ed					Append	ix 4.1. continued
Ref no.	Family	Subfamily	Genus/Species	Habitat other than forest floor	Singleton	•	Ref no.	Family
7	Carabidae	Bembidiinae	Tachys sp. (?) nov.				206	Carabidae
125	Carabidae	Bembidiinae	Tachys (<i>Polyderis</i>)				206B	Carabidae
			cf. captus				206C	Carabidae
			(Blackburn)				208	Carabidae
209	Carabidae	Bembidiinae	Pericompsus					
			seticollis Sloane				174	Carabidae
209	Carabidae	Bembidiinae	Tachys mitchelli				77	Carabidae
			Sloane					
54	Carabidae	Brachininae	Pheropsophus					
			verticalis Dejean				77	Carabidae
25	Carabidae	Broscinae	Promecoderus					
			concolor Germair				189	Carabidae
25	Carabidae	Broscinae	Promecoderus cf.				224	Carabidae
-			gracilis Germair					
168	Carabidae	Carabinae	Calosoma ·		1		173	
			(?)schayeri Erichson					
157	Carabidae	Chlaeniinae	Chlaenuis					
			darlingensis				197	Carabidae
			Castelnau					
86	Carabidae	Harpalinae	Lecanmerus				232	Carabidae
			discoidalis					
			(Blackbrun)				35	Carabidae
203B	Carabidae	Harpalinae	Egadroma piceum					
			Guérin				71	Carabidae
145	Carabidae	Harpalinae	Egadroma sp.	Not pitfall trapped;	✓			
				in logs only				
							201	Carabidae

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151 Carabidae

230

Subfamily	Genus/Species	Habitat other than	Singleton
		forest floor	
Harpalinae	Lecanomerus sp.		
Harpalinae	Lecanomerus sp.		
Harpalinae	Lecanomerus sp.		
Harpalinae	Amblystomus nr.		
	palustris Blackburn		٤.
Harpalinae	(?)Amblystomus sp.	.	·
Lebiinae	Microlestodes		
	australiensis		
	(Sloane)		
Lebiinae	Microlestodes		
	<i>macleayi</i> (Csiki)		
Lebiinae	(?)Microlestodes sp.		
Lebiinae	Anomotarus minor		
	Blackburn		
Lebiinae	Anomotarus nr.		
	tumidiceps		
	Blackburn		
Lebiinae	(?)Agonochila sp.	Not pitfall trapped;	1
	,	in skirt traps only	
Lebiinae	Trigonothops sp.	Not pitfall trapped;	1
		in skirt traps only	
Licininae	Microferonia cf.		
	adelaide Blackburn	· · · · ·	
Licininae	Dicrochile		
	quadricollis		
	Castelnau		
Licininae	Dicrochile		
	<i>brevicollis</i> Chaudoir		
Licininae	Physoloesthus nr.		
	pallidus Blackburn		·

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Append	ix 4.1. continu	ied						Append	ix 4.1. continue	d
Ref no.	Family	Subfamily	Genus/Species	Habitat other than	Singleton			Ref no.	Family	
				forest floor						
27	Carabidae	Pentagonicinae	Scopodes aeneus					220	Carabidae	
			Macleay			}				
27B	Carabidae	Pentagonicinae	Scopodes sigillatus					204	Carabidae	
			Germair							
8	Carabidae	Pterostichinae	Simodontus sp. (nr.					204	Carabidae	
		•	australis)					200	Carabidae	
3	Carabidae	Pterostichinae	Sarticus	×						
			discopunctatus							
			Chaudoir					84B	Carabidae	
9A	Carabidae	Pterostichinae	Platycoelus prolixus							
			(White)				· · · · · · · · · · · · · · · · · · ·	200B	Carabidae	
9B	Carabidae	Pterostichinae	Playcoelus melliei							
			(Montrouzier)					205	Carabidae	
)	Carabidae	Pterostichinae	Catadromus							
			lacordairei					134	Carabidae	
			Boisduval					195	Cerambycidae	
	Carabidae	Pterostichinae	Pseudoceneus							
			sollicitus (Erichson)							
r.	Carabidae	Pterostichinae	Rhytisternus					76	Chrysomelidae	
			liopleurus			l		114	Chrysomelidae	
			(Chaudoir)					15	Chrysomelidae	
В	Carabidae	Pterostichinae	Rhytisternus					135	Chrysomelidae	
			laevilaterus					120	Chrysomelidae	
			(Chaudoir)			l		10	Chrysomelidae	
)2	Carabidae	Pterostichinae	Loxandrus					98	Chrysomelidae	
			subiridescens			-		5	Chrysomelidae	
			(Macleay)					37	Chrysomelidae	
l	Carabidae	Psydrinae	Mecyclothorax					149	Chrysomelidae	
			punctipennis							
			(Macleay)							
ł	Carabidae	Scaritinae	Clivina			:		154	Chrysomelidae	
			quadratifrons Sloane					-		
		· · · · · · · · · · · · · · · · · · ·						182	Chrysomelidae	

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Subfamily	Genus/Species	Habitat other than	Singleton
		forest floor	
Scaritinae	Geoscaptus	·····	·
	laevissimus Chaudoir		
Scaritinae	Clivina basalis		
	Chaudoir		
Scaritinae	Clivina felix Sloane		
Scaritinae	Clivina nr.		
	australasiae		
	Bohemann		
Scaritinae	Clivina nr. procera		
	Putzeys		
Scaritinae	Clivina nr. misella		
	Sloane		
Scaritinae	Clivina nr.		
	heterogena Putzeys		
			1
Cerambycinae	Phoracantha	Not pitfall trapped;	1
	semipunciata	in skirt traps only	
	Fabricius		
Galerucinae	Aulacophora sp.	Skirt traps.	
Galerucinae	(?)Menippus sp.		
Galerucinae	(?)Oides sp.	Skirt traps.	
Galerucinae	(?)Oides sp.	•	1
Galerucinae		Skirt traps.	е. — ¹
Hispinae	?		1
Hispinae			
		Skirt traps,	
		Not pitfall trapped;	
		in skirt traps and	
		logs only	
		Not pitfall trapped;	1
		in skirt traps only	
			1

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Ref no.	Family	Subfamily	Genus/Species	Habitat other than	Singleton	
				forest floor		
95	Cleridae					
196	Cleridae	Clerinae		Not pitfall trapped;	1	
				in skirt traps only		
196	Cleridae	Clerinae	(?)Phlogistus sp.	Not pitfall trapped;	1	
				in skirt traps only		
61	Coccinellidae	Coccinellinae	Coccinella			
			transversalis			
			Fabricius			
64	Coccinellidae	Scymninae	Diomus sp.			
142	Coccinellidae	Scymninae	Diomus sp.	Not pitfall trapped;		
				in skirt traps only		
43	Corylophidae	Sericoderinae	Sericoderus sp.			
176	Corylophidae	Sericoderinae	Sericoderus sp.		1	
14	Cryptophagidae		?	Skirt traps.		
	(?)			-		
19	Curculionidae	Amycterinae	(?)Cubicorhynchus			
			sp.			
34	Curculionidae	Amycterinae	Talaurinus howittii	Logs		
			Macleay			
128	Curculionidae	Amycterinae	(?)Phalidura sp.		1	

Bagous adelaidae

Sitona discoideus

(Gyllenhal)

Desiantha sp.

Sitophilus sp.

Pascoe

Ethemaia sellata

Elleschodes sp.

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Appendix 4.1. continued

Family

Curculionidae

Dermestidae

Dytiscidae

Elateridae

Ref no.

51B

51C

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105

105B

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115

136

153

155

156

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162

164

175

186

188

193

194

199

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223

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240

17/87

39

16

218

38

51

Appendix 4.1. continued

Curculionidae

Curculionidae

Curculionidae

Curculionidae

Curculionidae

Curculionidae

Curculionidae

Amycterinae

Bagoinae

Entiminae

Erirhininae

nae

Rhynchophori

Rhytirhininae

Tychinae

Subfamily	Genus/Species	Habitat other than	Singleton
		forest floor	
Tychinae	Emplesis sp.		<u> </u>
Tychinae	Emplesis sp.	Not pitfall trapped;	
		in skirt traps only	
			· L
			1
			*
			v
		Skirt traps.	
		Not pitfall trapped;	1
		in skirt traps only	
		Not pitfall trapped;	
		in skirt traps only	
		Not pitfall trapped;	1
		in skirt traps only	
		Not pitfall trapped;	
		in skirt traps only	
			1
			1
			1
		Skirt traps.	
		Not pitfall trapped;	1
		in skirt traps only	
		Not pitfall trapped;	
		in skirt traps only	
		Not pitfall trapped;	1
		in logs only	
	Orphinus sp.	Log	,
Colymbetinae	Rhantus (?)suturalis		√
_	Macleay		
Pyrophorinae	(?) Agrypnus sp.	Skirt traps.	

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Append	lix 4.1. continued							Append	ix 4.1. continued
Ref no.	Family	Subfamily	Genus/Species	Habitat other than	Singleton	•		Ref no.	Family
				forest floor					
69	Elateridae	Руторногіпае	Conoderus sp.	<u></u> *		•		116	Mycetophagidae
:30	Elateridae		Anilicus xanthomus	Not pitfall trapped;	1			101	Nitidulidae
			Macleay	in skirt traps only				72	Nitidulidae
57	Elateridae			Skirt traps.				217	Nitidulidae
<i>i</i> 8	Elateridae							217	Nitidulidae
215	Histeridae	Saprininae	Saprinus sp.					3	Nitidulidae
:21	Histeridae	Tribalinae	Stictostix sp.						
242	Histeridae	(?)Histerinae			√			190	Cedemeridae
12	Hydraenidae		Hydraena		√			192	Oedemeridae
			luridipennis Macleay						
131	Hydraenidae		Ochthebius sp.					12	Pselaphidae
74	Hydrophilidae	Hydrobiinae	Helochares sp.					21	Psetaphidae
5	Hydrophilidae	Hydrobiinae	Enochrus sp.					80	Pselaphidae
221	Hydrophilidae	Hydrobiinae	Hydrophilus sp.		\checkmark			80B	Pselaphidae
33	Laemophloeidae		Cryptolestes sp.						
20/55	Lathridiidae	Corticariinae	(?)Corticarina sp.						
37	Lathridiidae	Corticariinae	(?)Corticarina sp.	Skirt traps.				24	Pselaphidae
53	Lathridiidae	Lathridiinae	Aridius sp.		√			48	Pselaphidae
52	Lathridiidae	Lathridiinae	Aridius sp.		√			29	Pselaphidae
I	Leiodidae	Cholevinae	Nargomorphus sp.					113	Pselaphidae
216	Leiodidae	Cholevinae	(?)Cholevomorpha					163	Pselaphidae
			sp.					13	Pselaphidae
50/41	Leiodidae	Coloninae	Colon sp.						
236	Lucanidae	Nicaginae	Ceratognathus sp.		1			129	Pselaphidae
			(nr. westwoodi)					150	Pselaphidae
166	Lycidae		Metiorrhynchus sp.		1				-
140	Melyridae	Malachiinae	Dicranolaius sp.		1			213	Pselaphidae
743	Mahrridaa	Malachiinaa	Diananalaina an					214	Pselaphidae
,	MEITINGE	14191901111190	истановано зр.					165	Ptinidae
178	Meluridae	Malaahiinaa	Ralanonhominon			`		231	Ptinidae
270 R1	Mordallidaa	Mordallingo	Hoshikananomia or					59	Scarabaeidae
· 4		Mordennae	nosninananomia sp.	<u></u>				122	Scarabaeidae
							2	173	Scarahaeidae

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Subfamily	Genus/Species	Habitat other than	Singleton		
		forest floor			
	Litargus sp.				
Carpophilinae	Carpophilius sp.				
Cillaeinae	Brachypeplus sp.	Skirt traps.			
Cillaeinae	Brachypeplus sp.				
Cillaeinae	Brachypeplus sp.		1		
Nitidulinae	Thalycrodes austale				
	(Germar)				
Oedemerinae	(?)Copidita sp.				
Oedemerinae	Copidita sp.	Not pitfall trapped;	1		
		in skirt traps only			
Clavigerinae	Articerus sp.				
Clavigerinae	Articerus sp.				
Clavigerinae	Articerus sp.				
Clavigerinae	Articerus sp.	Not pitfall trapped;	1		
		in logs only			
Clavigerinae	Rybaxis sp.		√		
Clavigerinae	Rybaxis sp.		1		
Clavigerinae	Euplectops sp.		1		
Clavigerinae	(?)Euplectops sp.				
Clavigerinae	(?)Euplectops sp.		1		
Pselaphinae	Pselaphaulax				
	(?)pilosus Reitter				
Pselaphinae	Eupines sp.		, s		
Pselaphinae	(?)Hamotpsis sp.	Not pitfall trapped;	1		
		in logs only			
Pselaphinae	Ctenisophus sp.		1		
Pselaphinae	<i>Tyraphus</i> sp.		\checkmark		
Ptininae	Ptinus sp.	Skirt traps.			
Ptininae	Ptinus sp.				
Aphodiinae	Aphodius sp.				
Melolonthinae	Heteronyx sp.				
Melolonthinae	(?)Liparetrus sp.		√		

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Appendix 4.1. continued

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Ref no.	Family	Subfamily	Genus/Species	Habitat other than	Singleton
				forest floor	1
184	Scarabaeidae	Melolonthinae	(?)Phyllotocus sp.		·
180	Scarabaeidae				\checkmark
181	Scarabaeidae				1
171	Scraptiidae	Scraptiinae	Scraptia sp.		
4	Scydmaenidae		(?)Neuraphoconnus		
			sp.		
82	Silvanidae	Silvaninae	Ahasverus sp.	Skirt traps.	
234	Silvanidae	Silvaninae	Silvanus (?)lateritius		1
			Broun		
226	Silvanidae	Uleiotinae	Cryptamorpha sp.		
2	Staphylinidae	Aleocharinae			
117	Staphylinidae	Aleocharinae			
73	Staphylinidae	Aleocharinae			
100	Staphylinidae	Aleocharinae	<i>Falagria</i> sp.		
	Staphylindiae	Aleocharinae		Not pitfall trapped;	
				only in logs with	
				nests of	
				Coptotermes	
				acinaciformis	
				(Froggatt)	
58	Staphylinidae	Omaliinae			
92	Staphylinidae	Omaliinae	(?)Hapalarea sp.		
58	Staphylinidae	Oxytelinae	(?)Anotylus sp.		
89	Staphylinidae	Oxytelinae	Anotylus sp.		
89B	Staphylinidae	Oxytelinae	Anotylus sp.		
97	Staphylinidae	Paederinae	Scymbalium	Skirt traps.	
			(?)australicum		
			Solsky		

Appendix 4.1. continued

Ref no.	Family
118	Staphylinidae
127	Staphylinidae
185	Staphylinidae
237	Staphylinidae
212	Staphylinidae
244	Staphylinidae
85	Staphylinidae
108	Staphylinidae
65	Staphylinidae
66	Staphylinidae
66B	Staphylinidae
22	Staphylinidae
	Staphylindiae
146	Staphylinidae
42	Staphylinidae
62	Staphylinidae
207	Staphylinidae
241	Staphylindiae
8	Staphylinidae
8B	Staphylinidae
8C	Staphylinidae
22B	Staphylinidae
22C	Staphylinidae
132	Staphylinidae
147	Staphylindiae
233	Tenebrionidae

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Subfamily	Genus/Species	Habitat other than	Singleton
		forest floor	
Paederinae	Scopaeus sp.	······································	
Paederinae	Lathrobium sp.		
Paederinae			
Paederinae			1
Paederinae	Dicax sp.		
Paederinae			5
Pinophilinae	Pinophilus sp.		
Pinophilinae	Pinophilus sp.		1
Quediinae	(?)Quedius sp.		
Quediinae	(?)Quedius sp.		
Quediinae	(?)Quedius sp.		
Staphylininae			
Steninae	Stenus puncticollis		1
	Macleay		
Tachyporinae	(?)Tachinus sp.	Logs	
Tachyporinae	Tachinus sp.		
Xantholininae	(?)Thyreocephalus		
	sp.		
Xantholininae	Threocephalus sp.		
Xantholininae	Zeteotomus sp.		1

Alleculinae

Nocar depressiusculus Macleay

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Not pitfall trapped; only in logs Not pitfall trapped; only in skirt traps

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Appendix 4.1. continued								
Ref no.	Family	Subfamily	Genus/Species	Habitat other than	Singleton			
				forest floor				
138	Tenebrionidae	Lagriinae	Pterohelaeus sp.					
222	Tenebrionidae	Lagriinae	Pterohelaeus sp.		1			
170	Tenebrionidae	Lagriinae	Celibe sp.		1			
187	Tenebrionidae	Lagriinae	Chalcopteroides sp.	Not pitfall trapped;				
				only in logs				
90	Tenebrionidae							
141	Throscidae		Aulonothroscus	Not pitfall trapped;				
			(?)elongatus	only in skirt traps				
			Bonvouloir					
167	Trogidae		Omorgus sp.		√			
32	Trogossitidae	Lophocaterin	Neaspis sp.					
		-ae						
28								
124								
179								
210#	Carabidae	Bembidiinae	Bembidion proprium					
			Blackburn					
203#	Carabidae	Harpalinae	Euthenarus nr.					
			morganensis					
			Blackburn					
202#	Carabidae	Ooodinae	Oodes modestrus					
			Castelnau					
44*	Curculionidae	Rhytirhininae	Ethemaia (?)adusta					
			Pascoe					
47*	Curculionidae	Aterpinae	Ophthalmorhychus		1			
			sp.					
45*	Silvanidae	Uleiotinae	Cryptamorpha sp.		√			
46*	Salpingidae	Lissodeminae	Neosalpingus sp.		1			

Denotes beetles caught on channel edges or moira-grass wetlands in November 2002 (only Carabidae analysed.)

*Denotes species captured only in August surveys and not included in any data analysis.

Appendix 4.2. List of spe January 2003. (Ref. no. 1 the voucher collection.)

Ref no.	Family	Genus/Species	Present	Present	Present	Singleton
			forest	logs	skirt	
			floor		traps	
41	Amaurobiidae		-	-		✓
89	Amaurobiidae		✓			
149	Amaurobiidae			✓		
198	Amaurobiidae				✓	✓
159	Araneidae				✓	
159B	Araneidae				✓	
159c	Araneidae				✓	
160	Araneidae	Dolophones sp.			✓	
186	Araneidae				✓	
187	Araneidae	Dolophones sp.			✓	
222	Araneidae				✓	✓
228	Araneidae	Dolophones sp.			✓	✓
142	Clubionidae				1	
152	Clubionidae				✓	
153	Clubionidae				✓	
156	Clubionidae				✓	
158	Clubionidae				✓	
166	Clubionidae				✓	✓
183	Clubionidae				✓	
96	Clubionidae		1			
6/6b	Corinnidae	Supunna picta	1	✓	*	
		(Koch)				
43	Corinnidae		•		v	
	(Castianierinae)					
43B	Corinnidae		✓			
	(Castianierinae)					

Appendix 4.2. List of species of Araneae captured in Barmah Forest, May 2000– January 2003. (Ref. no. refers to a reference number used to identify morphospecies in

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Ref no.	Family	Genus/Species	Present	Present	Present	Singletons
			forest	logs	skirt	
			floor		traps	
93	Corinnidae	······································	✓			
	(Castianierinae)					
105/32/134	Corinnidae	Idiospunna 'fusca'	✓		✓	
		sp. nov. Raven &				
		Stumkat				
		(Manuscript name)				
115	Corinnidae		1			4
	(Castianierinae)					
215	Ctenidae		1			√
29	Cyatholipidae	<i>Matilda</i> sp.	1			
			,	,	,	
8	Dictynidae		*	~	~	
	(Dicyninae)					
132	Dictynidae					
	(Dicyninae)					
116	Filistatidae		v			
130	Gallieniellidae	Meedo cohuna	1			
		Platnick				
35	Gallieniellidae		1			
40	Gnaphosidae		√			
42	Gnaphosidae		~			
	((?)Drassodinae)					
71	Gnaphosidae		√			
73	Gnaphosidae		v			
82	Gnaphosidae		\checkmark	✓		

Ref no.	Family	Genus/Species	Present forest floor	Present logs	Present skirt traps	Singleton
86/170female	Gnaphosidae		1			
95/170male	Gnaphosidae		1			
120	Gnaphosidae		✓			
125	Gnaphosidae		1			
133	Gnaphosidae		1			
135	Gnaphosidae		1			
137	Gnaphosidae		1			1
138	Gnaphosidae		1			1
140	Gnaphosidae		1			
171	Gnaphosidae		1	✓		
174	Gnaphosidae		1			
177	Gnaphosidae		1	✓		
182/217	Gnaphosidae				✓	
199	Gnaphosidae				1	
205	Gnaphosidae			~		
210	Gnaphosidae		✓			1
219	Gnaphosidae				✓	
220	Gnaphosidae				✓	✓
230	Gnaphosidae		✓			✓
234	Gnaphosidae		1			
235	Gnaphosidae		1			✓
223	Gnaphosidae	<i>Eilica</i> sp.			✓	1
	(Laroniinae)	-				
100	Gnaphosidae	Hemicloea sp.	1		✓	
	(Hemicloeinae)					
150	Gnaphosidae	Hemicloea sp.		1	✓	
	(Hemicloeinae)	-	·			

Appendix 4.2. con	tinued
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Ref no.	Family	Genus/Species	Present	Present	Present	Singletons
			forest	logs	skirt	
			floor		traps	
18	(?)Hahniidae		~			
31	Hahniidae		✓			
-	(Hahniinae)					
31B	Hahniidae		✓			
	(Hahniinae)					
31C	Hahniidae		✓			
	(Hahniinae)					
175	Hahniidae		✓			
	(Hahniinae)					
163	Hersiliidae	Tamopsis sp.			1	
163 B	Hersiliidae	Tamopsis sp.			✓	
34	Lamponidae	Asadipus	✓			
	(Centrothelinae)	kunderang Platnick				
7 9	Lamponidae		✓			
131/178	Lamponidae		✓	✓		
	(Centrothelinae)					
206	Lamponidae		~			
214	Lamponidae		✓			
	(Lamponinae)					
10	Linyphiidae		✓			
	(Erigoninae)					

Appendix 4.2. continued

Ref no.	Family	Genus/Species	Present	Present	Present	Singletons
			forest	logs	skirt	
			floor		traps	
83	Linyphiidae	Erigone	1	·	1	·
	(Erigoninae)	(?)dentipalpis				
		(Wider)				
216	Linyphiidae				✓	
	(Erigoninae)					
41	Linyphiidae		✓			
	((?)Erigoninae)					
52/58	Linyphiidae		✓	✓		
	(Erigoninae)					
69	Linyphiidae		✓			
	(Erigoninae)					
148	Linyphiidae		1			
	(Erigoninae)					
188	Linyphiidae				4	
	(Erigoninae)					
203	Linyphiidae				1	✓
	(Erigoninae)					
213	Linyphiidae		1			1
	(Erigoninae)					•
14	Linyphiidae		✓			
	((?)Linyphiinae)					
30/94/76	Linyphiidae		✓			
	((?)Linyphiinae)					
54	Linyphiidae		✓			
	(Linyphiinae)					
157/191	Linyphiidae		✓			
	(Linyphiinae)					
5	Lycosidae	Lycosa (nr.	1	1		
		alteripa)			-	
23	Lycosidae	Allocosa	✓		· .	
		palabunda (Koch)				

Appendix 4	.2. continued						Appendix 4	.2. continued					
Ref no.	Family	Genus/Species	Present	Present	Present	Singletons	Ref no.	Family	Genus/Species	Present	Present	Present	Singletons
			forest	logs	skirt					forest	logs	skirt	
•			floor		traps					floor		traps	
23A	Lycosidae	Venatrix spenceri	~		<u> </u>	v	151/208	Lycosidae	Venatrix goyderi	~			
		(Hogg)	-						(Hickman)				
49	Lycosidae	Artoria	✓				173	Lycosidae	Artoria sp.	✓			✓
		'victoriensis' sp.							[undescribed]				
		nov.					51	Miturgidae	Uliodon	\checkmark			
									(?)tarantulinus				
		Framenau, Gotch &							(Koch)				
		Austin (manuscript					231	Miturgidae		✓			
		name)					110	Miturgidae		✓			
49B/90	Lycosidae	Venatrix	~		1		2	Oonopidae	<i>Opopaea</i> sp.	✓	✓		
		pseudospeciosa					117	Oonopidae	Grymeus yanga	✓	√		
		Framansus & Vink							Harvey				
66	Lucosidos	Anomalasa kochi	1				127	Oonopidae	<i>Myrmopaea</i> sp.	✓			
00	Lycosidae	(Simon)	•				127B	Oonopidae	Ischnothryreus sp.	✓			
Q.4	Lucosidoo	(Simon)	1				113	Oxyopidae		✓			
04	Lycosidae	(impodita)	•		·		46	Pararchaeidae	Pararchaea sp.(nr.	✓			
		(Infeatia)							binnaburra) Walker				
100/124	Lucosidos	(L.Koch)	1				55	(?)Pisauridae		✓			✓
109/124	Lycosidae	nogna	•				85	Pisauridae	(?)Dolomedes sp.	✓			
		(Strand)					87/44	Prodidomidae		✓	1		
111/170	Lycosidoe	(Suanu)	1	1	1			(Molycriinae)					
111/1/2	Lycosidae	howauaansis	·	•	·		36/36B	Salticidae	' 'Lycidas' sp.	✓		1	
		nowquaensis						(Unidentati)					
		Framenau					101	Salticidae	(?)Helpis sp.	✓			
112	Lycosidae	Lycosa leukartii	✓		1			(Pluridentati)					
		(Thorell)					108 (may be	Salticidae	Clynotis sp.	✓		1	
136	Lycosidae	Venatrix fontis	✓			✓	129)	(Unidentati)					
		Framenau & Vink					114/233	Salticidae	Maratus sp.	✓	✓		
	<u> </u>				<u></u>			(Unidentati)					
							123	Salticidae	Myrmarachne sp.			1	V
								(Pluridentati)					
							126	Salticidae	(?)Maratus sp.	✓			1
								(Unidentati)				•	

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Appendix 4	.2. continued					
Ref no.	Family	Genus/Species	Present	Present	Present	Singletons
			forest	logs	skirt	
			floor		traps	<u></u>
28	Salticidae	(?)Hypoblemum sp.	✓		1	
	(Unidentati)					
29	Salticidae	(?)Clynotis sp.				
	(Unidentati)					
44	Salticidae			1	1	
	(Fissidentati)					
154	Salticidae	Bianor			✓	✓
	(Unidentati)	(?)maculatus				
		(Keyserling)				
55	Salticidae	<i>Servaea</i> sp.			1	
	(Fissidentati)					
61	Salticidae	Rhombonotus sp.			✓	1
	(Pluridentati)					
61B	Salticidae	Damoetas sp.			1	1
	(Pluridentati)					
62	Salticidae	Simaethula sp.			1	
	(Fissidentati)					
.65	Salticidae	(?)'Trite' sp.			✓	
	(Unidentati)					
69/192	Salticidae	Ocrisiona sp.			✓	
	(Unidentati)					
72/36B	Salticidae	Lycidas sp.	✓			
	(Unidentati)	-				
80	Salticidae				1	
	(Pluridentati)					
81	Salticidae	Clynotis sp.			1	
	(Unidentati)	-				
184	Salticidae	Cytaea sp.			✓	
	(Fissidentati)	-				

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Appendix 4.2. continued

Ref no.	Family	Genus/Species	Present	Present	Present	Singletons
			forest	logs	skirt	
			floor		traps	
189	Salticidae	Gangus (Thyrene)			1	√
	(Unidentati)	sp.				
190	Salticidae	Sandalodes sp.			✓	
	(Unidentati)					
193	Salticidae				✓	 Image: A set of the set of the
	(Unidentati)					
195	Salticidae	Astia sp.			✓	✓
	(Pluridentati)					
196	Salticidae	Holoplatys sp.			✓	
	(Unidentati)					
200	Salticidae				✓	✓
	(Unidentati)					
201	Salticidae	Lycidas sp.			✓	
	(Unidentati)					
204	Salticidae	(?)Clynotis sp.	✓	✓		
	(Unidentati)					
204/227	Salticidae	Arasia			✓	
	(Pluridentati)	(?)mollicoma				
		(Koch)				
218	Salticidae	(?)Helpis sp.			1	
	(Pluridentati)					
194	Sparassidae				✓	✓
232	Sparassidae					
221	Tetragnathidae	(?)Tetragnatha sp.			✓	
	(Tetragnathinae)					
12	Theridiidae	Hadrotarsus	✓			
	(Hadrotarsinae)	(?) <i>fulvus</i> Hickman				
12B	Theridiidae	Hadrotarsus sp.	✓		:	
	(Hadrotarsinae)					
47	Theridiidae		✓	✓	✓	
	(Phoroncidiinae)					

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$\pi \mu \mu$	Append	ix 4.2	. contin	ued
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Ref no.	Family	Genus/Species	Present	Present	Present	Singletons
			forest	logs	skirt	
			floor		traps	
81	Thomisidae		1		~	
143	Thomisidae	(?)Tharpyna sp.	•		1	
185	Thomisidae	(?)Tharpyna sp.			1	
202	Thomisidae				✓	✓
	(Stephanopsinae)					
226	Thomisidae				1	*
229	Thomisidae				· 🗸	✓
59/121	Zoridae		1		1	
104	Zoridae	Argoctenus sp.	1	1	1	
9c	Zodariidae	Habronestes	1			
		grahami Baehr				
88/106	Zodariidae	Habronestes raveni	1			
		Baehr				
28	Zodariidae	Neostorena sp. nov.	1			
139/139Ъ	Zodariidae	Pentasteron	1	1		
		intermedium Bachr				
		& Jocque				
207	Zodariidae	Holasteron sp. nov.	~			1
		Baehr				

CHAPTER FIVE THE EFFECT OF FLOODING ON THE STRUCTURE AND STABILITY OF ANT (HYMENOPTERA: FORMICIDAE) ASSEMBLAGES IN RIVER RED GUM **EUCALYPTUS CAMALDULENSIS FLOODPLAIN** FOREST

Abstract

The ant fauna in river red gum *Eucalyptus camaldulensis* forest was surveyed before and for 2 yr after a major flood to identify the effects of flooding on ground-active ant assemblages. The abundance and species richness of ground-active ants were greatest in the least flood-prone areas. Moreover, flooding consistently produced a characteristic ant assemblage in the short-term. In flood-prone areas, species turnover was lower than in dry areas, but the relative abundance of species comprising assemblages changed more rapidly. Therefore, flooding can be perceived as either a stabilizing or a de-stabilizing process, depending on the metric used to assess stability.

The abundance and species richness of ants differed between sites with different localized flood regimes before the major flood, suggesting that persistent habitat changes associated with long-term flood patterns may regulate ant assemblages. Competitive *Iridomyrmex* (Dominant Dolichoderinae) was the most commonly trapped group in all areas. Dominant Dolichoderinae comprised a greater proportion of the ant fauna in the most flood-affected areas, despite flooding not creating a more open habitat structure that is favoured by *Iridomyrmex*. Thus, flood disturbance does not release ants from competition. Ant predators (zodariid spiders) were relatively more abundant on drier sites. Therefore, different biotic regulatory processes are disrupted by disturbance (flooding) to differing extents. Intensity of competition is less affected by disturbance than is predation and may be a more influential process in disturbance-prone areas.

Introduction

Floodplains are highly variable habitats that alternate between aquatic and terrestrial phases (Junk 1996). Flood perturbation is considered by some ecologists to induce a recovery period in riparian biota, followed by a quasi-equilibrial state (e.g. Décamps 1993; Molles *et al.* 1998). However, Oberdorff *et al.* (2001) demonstrated that increased flow variability was positively correlated with variability in riverine fish assemblages. Oberdorff *et al.* (2001) contended that increased variability reduces species richness by increasing local extinctions. Decreased persistence rates resulted in higher species turnover (Oberdorff *et al.* 2001). The corollary of the findings of Oberdorff *et al.* (2001) is that areas of floodplain subjected to the greatest flood perturbation and, therefore, to the highest environmental variability, are expected to have the least temporally similar fauna.

Few studies have tracked floodplain organisms over time to provide empirical evidence for the existence of a steady state (but see Molles *et al.* 1998). Maintenance of a quasiequilibrial state necessitates some form of abiotic or biotic regulation that extends beyond the inundation period. Flooding could impose long-term constraints on the floodplain biota by creating persistent differences in habitat structure. Alternatively, flooding might release organisms from intense biotic regulation. Frequent perturbation is viewed as reducing regulatory biotic interactions, such as competition and predation (Connell 1978). Resolving whether flooding ultimately stabilizes or destabilizes biotic assemblages is important for understanding the ecology of river-floodplain systems.

Ground-nesting ants lend themselves as study organisms to investigate flood-associated regulation of fauna. The important contribution of ants to biodiversity, animal biomass and ecosystem processes, particularly soil engineering, has been documented in many studies (see review by Folgarait 1998). Moreover, ant assemblages typically exhibit marked and predictable responses to disturbance (Andersen 1999). Generally, flooding is highly disruptive to ground-nesting ants. Sheppe and Osborne (1971) found no ant nests in frequently inundated grassland on a Zambian floodplain. On forested floodplains, increased flood proneness is correlated with lower ant diversity (Wilson

1987; Majer and Delabie 1994; Milford 1999; Adis and Junk 2002). However, for species that can cope with flooding, riparian zones potentially provide 'rich pickings' for scavenging ants, with allochthonous inputs of (aquatic) prey (Hering 1995). Furthermore, the higher productivity associated with riparian zones might support a greater density of terrestrial food sources.

In south-eastern Australia, river red gum *Eucalyptus camaldulensis* Denhn. forms extensive floodplain forests in the Murray-Darling Basin. These floodplain forests have existed in their current form for 10 000 years (Bowler and Harford 1966)—a short period in evolutionary time. Natural and regulated flood regimes in river red gum forests are highly variable (Bren *et al.* 1987). The unpredictability and short history of river red gum forests are not expected to have been conducive to the development of a highly specialized floodplain ant fauna. However, the river red gum floodplain forests occur in an overlap region where the arid-zone fauna abuts the cooler mesic-zone fauna, potentially creating a rich assemblage able to exploit the high habitat variability (*sensu* Andersen 1984; Hinkley and New 1997).

Andersen (1997) and Milford (1999) found that ant species classified as opportunistic numerically dominated floodplain-forest ant assemblages in the south-western USA. Opportunistic species comprised over 90% of the ants caught in pitfall traps by Andersen (1997). Disturbances generally are thought to reduce competition, favouring opportunistic species (Andersen and McKaige 1987). Opportunist species are characterized by having broad habitat ranges, generalized diets but poor competitive ability (Andersen 1995; 1997).

Opportunistic species might be expected to constitute the majority of ants in Australian riparian assemblages. However, the Australian ant fauna is dominated by a single genus, *Iridomyrmex* (Andersen 1997), despite being exceptionally species rich overall. The Australian *Iridomyrmex* comprises 63 described species, typified as aggressive, highly competitive and very abundant (Shattuck 1999). The genus is virtually ubiquitous in temperate Australia and has no equivalent in ant assemblages elsewhere in the world (Andersen 1997). Andersen (1991) and Vanderwoude *et al.* (1997) demonstrated that frequent fire disturbance increased *Iridomyrmex* domination of ground-foraging ant assemblages, rather than allowing the opportunistic species to

increase in response to release from competition. However, frequent burning also created a more open habitat structure, favoured by *Iridomyrmex*.

In contrast, Hoffman and Andersen (2003) reviewed ant-disturbance responses and found that *Iridomyrmex* decreased in response to disturbance that created densely shaded areas. Thus, the ability of *Iridomyrmex* to maintain competitive dominance in the face of disturbance could not be separated from response to habitat structural change *per se.* Examination of ant-assemblage responses to inundation would enable an assessment of the capacity of *Iridomyrmex* to maintain dominance in a disturbance-prone environment where favourable habitat change is absent.

In addition to reducing competition, disturbance is considered to reduce predation because consumers are more inhibited by disturbance than are prey (Menge and Sutherland 1976). Knobble spiders (Zodariidae) are specialized predators of ants (Bachr and Churchill submitted). The abundance and ubiquity of ants has allowed knobble spiders to reach high densities and richness in semi-arid Australia (Churchill 1997; Bachr and Churchill submitted). Spiders often regulate prey populations (e.g. Riechert and Lawrence 1997; Moran and Scheidler 2002), although I am not aware of any studies that specifically have addressed whether spiders regulate ant populations. A dynamic faunal state might result if ants in frequently flooded areas are released from regulation by predation.

The diversity of ants can be a barrier to understanding their ecology because having many different species with similar ecological characteristics in a system generates 'noise' in data sets. A functional-groups approach classifies species by behavourial traits, rather than by taxonomy and can be a powerful tool for analysis of invertebrate ecological data. Greenslade (1978) developed a functional-groups classification system for Australian ants, which was later improved and expanded to include North America fauna by Andersen (Andersen 1995; 1997). Ant functional groups have been used to analyze responses to various forms of disturbance, including grazing (Read and Andersen 2000; Woinarski *et al.* 2002), mining (Hoffmann *et al.* 2000) and managed burning (Vanderwoude *et al.* 1997).

Here, I characterize the ant assemblages in river red gum floodplain forest over 32 mo to determine whether the fauna achieved a quasi-equilibrial state after flooding. To identify whether competition is responsible for maintaining the quasi-equilibrial state, a functional-groups approach is used to measure changes in the abundance of competitive and opportunistic species in response to flooding. Last, the relative abundance of predators (zodariid spiders) to ant prey is compared between flood-prone and drier sites to assess the level of regulation of floodplain ant assemblages by predation.

Methods

Study area

This work was conducted in Barmah State Forest and Barmah State Park in northern Victoria, Australia, about 215 km from Melbourne (35°55'S 145°08'E). Barmah Forest occurs on the Murray River floodplain where geomorphic activity in the last 20 000 years has constricted the river channel, reducing channel capacity and resulting in frequent flooding of the forest. The Murray River and many anastomosing creeks run through the forest.

Soils are stratified layers of clay overlaid by sand (Silvers 1993). Barmah Forest consists largely of monospecific stands of *Eucalyptus camaldulensis* with an understorey of grasses, rushes and sedges (Chesterfield 1986). Under natural flood regimes, high flows created by winter rainfall and spring snowmelt regularly fully flooded the forest (Bren 1988). Substantial regulation of the Murray River began in 1934 with the construction of the Hume weir and filling of Lake Hume. Regulation has reduced the frequency of flows associated with forest flooding and shifted the timing of flooding, so that there is an increased occurrence of small, summer floods and a reduction in winter and spring floods (Bren 1988).

Site selection and flooding of the study area

In May 2000, the initial Forest. This study w Consequently, study site ha⁻¹) fallen-timber loads fallen-timber areas. The higher levels of fallen tir

In May 2000, the initial 16 50 m \times 50 m study sites were selected throughout Barmah Forest. This study was designed to explore effects of fallen timber on fauna. Consequently, study sites were selected to have either high (> 50 t ha⁻¹) or low (< 10 t

ha⁻¹) fallen-timber loads. In January 2001, eight additional sites were selected in high fallen-timber areas. There was some confounding of study design because sites that had higher levels of fallen timber also were more flood-prone. Five of the low fallen-timber

sites experienced brief flooding and the remaining three were moderately flooded (definition below). Two high fallen-timber sites flooded briefly or not at all, five flooded moderately and the remaining nine flooded for an extended period. However, fallen-timber load was not found to relate to the abundance or species richness of ants (Chapter Three). Therefore, fallen timber is not considered as a factor in this chapter.

The last major floods in the study area prior to 2000-2001 were in 1992-1993, with less-extensive flooding occurring in 1996 (Barmah-Millewa Forum 2001). In the austral spring/summer 2000-2001, Barmah Forest experienced widespread flooding with much of the forest inundated by October 2000. Large tracts of forest remained inundated for several months, preventing sampling in November 2000. Floodwaters had receded by January 2001.

Because the degree of flooding experienced at each study site was not measured directly, a *post facto* measure of inundation was used. Study sites were rated as having experienced 'brief,' 'moderate' or 'extended' flooding based on the following suite of site characteristics:

- brief or no flooding: soil dry and compacted, ground cover of dry (i) grasses, no aquatic-insect pupal cases evident;
- (ii) moderate flooding: soil dry, ground covering generally of verdant grass but may be some dead aquatic plants present, few aquatic-insect pupal cases present, may be some silt deposited by floodwaters evident;
- extended flooding: damp soil, considerable growth of water plants, (iii) many pupal cases of aquatic insects attached to tree trunks, often extensive silt deposition, 'watermark' left on tree trunks.

The duration of flooding at each site could not be predicted when the sites were selected, so that the study design was unbalanced, with nine sites categorized as experiencing extended flooding, eight sites experiencing moderate flooding and the remaining seven sites were subjected to bilef or no flooding.

The following year, spring/summer 2001-2002, flooding in Barmah Forest was negligible and none of the study sites or their immediate surrounds were inundated. In spring/summer 2002-2003, moderate flooding occurred and three study sites were inundated by November. Floodwaters prevented access to one of the sites, so data from only two re-flooded sites were collected during the November 2002 survey. By January 2003, floodwaters had receded and one more study site showed evidence of brief flooding. Thus, four sites were categorized as experiencing a second flood, although the immersion phase was considerably shorter than in 2000-2001.

Sampling protocol

Sampling was conducted at the initial 16 sites in May 2000 and August 2000 and at all 24 sites in January 2001, May 2001, August 2001, November 2001, January 2002, November 2002 and January 2003.

Five pitfall traps each with an opening diameter of 75 mm and depth 95 mm were set on each study site. Traps were closed for ≥ 24 h following installation to counter possible 'digging-in' disturbance effects (Greenslade 1973). Pitfall traps then were filled with a 70% propanol: 5% glycerol: 25% water preservative solution and opened for five days and nights. In the laboratory, samples were sieved to 1 mm^2 and transferred to a 70%: 30% distilled water solution for storage. Samples were sorted to morphospecies. Expert taxonomic assistance was sought to identify taxa to the highest practicable taxonomic level (see acknowledgements). Note that because a large proportion of Australian invertebrate fauna is undescribed, species-level identifications are uncommon.

Data analysis

Both the frequency (Décamps 1993) and duration of inundation (Tockner et al. 2000) are thought to influence floodplain fauna. However, due to the unpredictable localized flood patterns, it was not possible to test the effects of both factors. These analyses focus on the effect of flood duration.

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Response of the abundance and species richness of ants to flood duration

The study was a repeated-measures design, with seven visits to the same study sites. However, eight sites were not visited until the third survey time (January 2001). Furthermore, three sites and four sites had to be excluded from the November 2002 and January 2003 analyses respectively because they flooded a second time. Conventional repeated-measures ANOVA designs do not deal well with large amounts of missing data, particularly when the data are missing in a fairly systematic fashion (Quinn and Keough 2002). In this study, flood-prone sites were more likely to be missing from the last two sampling periods. Bayesian analyses are amendable to utilizing all data, so these were used here. The Bayesian models were run using the WinBUGs (Version 1.4, Spiegelhalter *et al.* 2003) program, which computes the joint posterior probability distributions of the model parameters with the data. Uninformative, normal priors were used, so that the posterior distributions were dominated by the data.

To analyze the effect of the 2000–2001 floods on the abundance of ants at sites that experienced different durations of inundation, I used this model:

 $Y_{j(i)k} \sim \text{Normal} (\mu_{jk}, \sigma_{jk})$ $\mu_{j(i)k(l)} = \alpha_l \lambda_{k(l)} + \beta_i \pi_{j(i)} + \sigma_j + \sigma_{jk}$

Where Y is the natural logarithm of the number of ants caught at study site j at sample sample time k. The duration of inundation experienced in spring/summer 2000-2001 at study site j is denoted by i. l represents the 'season' (i.e. autumn/winter or spring/summer) during which the sample was collected. α models the effect of sampling in autumn/winter on Y and λ are elements of a matrix that identifies survey as being conducted in autumn/winter ($\lambda = 1$) or spring/summer ($\lambda = 0$). The β s model the effect of duration of local flooding in spring/summer 2000-2001 on Y, and π are elements of a matrix that identify sites as belonging to a particular flood treatment (brief, moderate or extended inundation). The σ_j are site random effects, while the σ_{jk} are site-repeated-survey random effects (Breslow and Clayton 1993).

To determine whether there was an overall difference in abundance of ants between sites that flooded for different lengths of time in 2000–2001, pairwise differences in β s were calculated. These calculations are analogous to *post hoc* pairwise comparisons in frequentist statistics, but without the interpretative complications involved with adjusting type-I error rates.

The overall pairwise comparisons could potentially obscure short-term differences created by flooding. To track the strength of flood response through time, the mean difference in Ys between flood treatments for each survey time: $\mu_{\delta Yk}$, was calculated by: $\mu_{\delta Yk} = 0.33 \times ((Y_{j=1k} - Y_{j=3k}) + (Y_{j=1k} - Y_{j=2k}) + (Y_{j=2k} - Y_{j=3k}))$

where:

j=1 denotes sites subject to brief/no inundation;
j=2 denotes sites subject to moderate inundation;
j=3 denotes sites subject to extended inundation

A variation on the model was used to examine the effect of flooding and season on the species richness of ants. Because the species richness of ants was likely to be Poisson distributed (i.e. consisted of small, non-negative integers), it was necessary to include a logarithmic link function in the model, such that:

For all model outputs, the mean, standard deviation and 95% credible intervals for the model parameters of interest (α , β and $\mu_{\delta Yk}$) were derived. I adopted the simple decision-making criterion of Mac Nally and Horrocks (2002) for drawing inferences. Bayesian analyses provide a posterior probability distribution for each of the model parameters, and combinations thereof, such as the difference between any two or more parameters. The proportion of the posterior probability distribution lying above zero is referred to as the posterior probability mass (PPM). When a model parameter has no effect on the dependent variable, the posterior probability distribution is centred on zero and the expected value of PPM is 0.50. Model parameters with \geq 90% of the posterior probability distribution lying above zero (i.e. PPM \geq 0.90) were considered to have a 'substantial' positive effect on the dependent variable (i.e. to increase the value of the

$$Y_{j(i)k} \sim \text{Poisson} (\mu_{jk})$$
$$\ln(\mu_{j(i)k(l)}) = \alpha_l \lambda_{k(l)} + \beta_j \pi_{j(i)} + \sigma_j + \sigma_{jk}.$$

dependent variable). For parameters with negative coefficients, $\ge 90\%$ of the posterior probability distribution lies below zero to be classed as 'substantial,' giving a PPM ≤ 0.10 .

Stability of ant assemblages in relation to flood-proneness

Three measures of stability of the ant assemblages were used: (1) species turnover; (2) assemblage composition change over time; and (3) consistency of short-term flood response (i.e. whether the second flood produced a similar assemblage structure to the first flood).

Species turnover is a measure of the repeated extinction and immigrations of species in ecological assemblages (MacArthur and Wilson 1967). To avoid seasonal effects, only January survey data were used to calculate species turnover. Species turnover was calculated for the periods January 2001–January 2002 and January 2002–January 2003 as:

$$(E+I)/(S_1+S_2)$$

where: *I* is the number of species present in the first survey, but absent from the second survey

E is the number of species absent in the first survey, but present in the second survey

 S_1 and S_2 is the total number of species recorded in the first and second survey respectively.

Species for which only a single individual was recorded over two consecutive January surveys were excluded from the analysis because they were considered too rare to be reliably detected in the sampling and, therefore, likely to artificially increase species turnover rates. To determine whether species turnover varied between sites subjected to different durations of inundation, I used this Bayesian model:

Where Y is the arcsine of species turnover of ants caught at study site j at sample time k, and i denotes the length of time that study site j was inundated in spring/summer 2000-2001. The β s model the effect of duration of local flooding in spring/summer 2000-2001 on Y, and π are elements of a matrix that identify sites as belonging to a particular flood treatment (brief, moderate or extended inundation). The σ_j are site random effects, while the σ_{jk} are site-repeated-survey random effects (Breslow and Clayton 1993). The 95% credibility intervals for the differences between pairwise comparisons of β s were calculated, as for the other Bayesian models.

To assess assemblage compositional changes over time, the PRIMER 5.1.2 statistical package (Clarke and Gorley 2001) was used to compute Bray-Curtis similarities from morphospecies-by-site matrices. Only the January data were used to make results comparable with those for species turnover. The choice of data transformation, prior to computation of similarity matrices, is determined by the relative weighting a researcher wishes to give to rare versus abundant species (Clarke and Warwick 1994). The analyses were done using a variety of transformations and the results differed according to the relative weighting transformations gave to abundance and presence-absence. I present the results from the square-root transformed data and the presence-absence data to demonstrate the influence different weightings have on the interpretation of the data. Separate analyses of similarities (ANOSIMs) were performed, each using 20 000 iterations. For every pairwise comparison in the ANOSIM, PRIMER computed an Rstatistic. The R-statistic is the difference between average within-group similarity and between-group similarity, standardized for sample size (Clarke and Warwick 1994). ANOSIMs were performed separately for each of the flood treatments with assemblages grouped by survey time (i.e. January 2001 vs. January 2002, January 2002 vs. January 2003).

 $Y_{j(i)k} \sim \text{Normal} (\mu_{jk}, \sigma_{jk})$ $\mu_{j(i)k} = \beta_j \pi_{j(i)} + \sigma_j + \sigma_{jk}$

Pearson correlation coefficients were calculated for the relationships between assemblage compositional change (*R*-statistics) and the duration of inundation. Duration of inundation was expressed as a categorical variable (1 = brief/no flooding, 2 = moderate flooding, 3 = extended flooding). Data from sites that flooded a second time in spring-summer 2002–2003 were excluded from all of the analyses above.

The consistency of short-term responses to flooding was assessed by using ANOSIM to compare the composition of assemblages in January 2003 at sites that were inundated for a second time during late 2002 with the composition of assemblages in January 2001 at sites that were inundated for different lengths of time during late 2000. A square-root transformation of the species-by-site data was used and \leq 20 000 iterations were performed for the randomization tests.

Long-term response of ant assemblages to flooding

To assess persistence of flood-associated differences in the composition of ant assemblages, ANOSIM was used to compare assemblages between sites inundated for different lengths of time in 2000–2001. Each survey time was analysed separately. The similarity values were generated from square-root transformed species-by-site matrices and $\leq 20\ 000$ iterations were performed for each randomization test.

Flood response of ant functional groups with different competitive abilities

A summary of Andersen's (1995) functional-groups classification system is provided in Table 5.1.

The Bayesian model defined previously for analysis of ant abundance was used with (1) the proportion of Dominant Dolichoderinae ants and; (2) the proportion of Opportunists as the dependent variable to identify seasonal and flood effects on those functional groups. In both cases, the proportion of the functional group was arcsine transformed to normalize Y_s .

Flood response of specialist ant predators, zodariid spiders

The ratio of the total number of ants to the total number of zodariid spidesr was calculated separately for every site for each January survey, with one extra spider being added to the denominator to allow the data from sites where no zodariid spiders were caught to be included in the analysis. Only the January data were used because most adult spider specimens were caught during summer surveys. Zodariid spiders might target specific ant species (cf. Greenslade and Halliday 1983), but as prey species were unknown, the total ant catch was considered to represent prey abundance. The Bayesian model used was the same as the species turnover model defined previously, except that the ratio of ants to zodariid spiders (natural-log-transformed) was the dependent variable.

Results

Response of the abundance and species richness of ants to flood duration

A total of 42 965 ants were pitfall trapped from 41 morphospecies and 19 genera (including sites that flooded in spring 2002) (Appendix 5.1). Abundance (ant activity) varied seasonally and not surprisingly, was lower in the autumn and winter surveys compared to the spring and summer surveys (Fig. 5.1, Table 5.2). Overall, ant abundance was not different between sites that experienced moderate or extended flooding in 2000-2001, but was greatest at sites subjected to brief or no flooding (Fig. 5.1, Table 5.2). Separate analysis of each survey period revealed that this pattern held before the 2000–2001 flood (Table 5.3).

Overall, the fauna was relatively species-poor. Species richness was greater in the spring and summer compared to autumn and winter, possibly as a result of larger catches in the spring and summer surveys (Fig. 5.2, Table 5.4). Species richness was greatest on dry sites, intermediate on sites subject to moderate flooding and least on sites subject to extended flooding (Fig. 5.2, Table 5.4). The consistency of this difference is borne out by the posterior probability masses for the mean difference (increase) in species richness at drier sites compared to sites experiencing longer inundation, which had a value of 1.0 for all survey times and hence, has not been tabulated.

Stability of ani assemblages in relation to flood-proneness

Ant assemblages at the sites that experienced moderate or extended inundation in 2000-2001 had substantially lower species turnover than drier sites when the 2001-2002 and 2000–2003 data were considered together (Table 5.5) and separately (Table 5.6).

For the square-root transformed data, the variability in assemblage structure of ants between summer 2001 and 2002, and between summer 2002 and 2003 was positively $(r^2 = 0.05, P \approx 0.68)$

In January 2003, the structure of assemblages at sites that flooded a second time in 2002-2003 was not different from the structure of assemblages in January 2001 at sites that experienced extended flooding in 2000-2001, suggesting that flooding may produce a characteristic fauna in the short-term (Table 5.7).

Long-term response of ant assemblages to flooding

Immediately after the recession of floodwaters, groups of sites that flooded for different lengths of time had different ant assemblages (Table 5.8). There was little evidence that ant assemblages diverged in response to flooding, at least over the study period (Table 5.8). The assemblages always differed between the groups of sites that experienced the longest flooding and the least flooding, except for in August 2000 when few ants were captured (Table 5.8). Assemblages at sites subjected to moderate and brief/no flooding initially appeared to have diverged in response to flooding and then to have converged, but the assemblages diverged again in January 2002 in the absence of further flooding (Table 5.8).

Flood response of ant functional groups with different competitive abilities

At all times, Iridomyrmex sp. (mattiroloi group), belonging to the Dominant Dolichoderinae functional group, formed a major component of the ant assemblages at both flood-prone and drier sites (Fig. 5.4 and 5.5). In January 2001, ants of the Dominant Dolichoderinae comprised over 90% of the total combined ants caught in areas that recently experienced prolonged inundation, although the 95% confidence

correlated with duration of flooding ($r^2 = 0.80$, $P \approx 0.016$) (Fig. 5.3). However, this relationship did not hold when the analysis was repeated using presence-absence data interval for the site mean was 66.3-97.5% due to variation in the numbers of ants trapped between sites.

Ants of the Dominant Dolichoderinae comprised a smaller proportion of the fauna in the cooler autumn and winter survey periods compared to the spring and summer surveys (Table 5.9). Calculation of the mean pair-wise differences in abundance revealed that Dominant Dolichoderinae were proportionally less abundant on drier sites at all survey times except August 2000, when the total catch was very low (Table 5.10).

Opportunists comprised a major element of the fauna (Fig. 5.4 and 5.5). In con⁺rast to Dominant Dolichoderinae, Opportunists constituted a larger component of the ant fauna in autumn and winter than in spring and summer (Table 5.11). Opportunists were proportionally more abundant at sites that experienced moderate flooding compared to sites that flooded briefly or not at all (Table 5.11). However, analysis of the results for individual surveys showed no consistent pattern in relation to flooding (Table 5.12).

Flood response of specialist ant predators (zodariid spiders)

Zodariid spiders were most abundant on the least inundated sites (Fig. 5.6). The ratio of ants to zodariid spiders was substantially lower on drier sites compared to sites that experienced mc, erate or extended inundation in 2000–2001 (Table 5.13). This relationship held both when the results from the January surveys were pooled (Table 5.13) and when the surveys were considered separately (Table 5.14).

Discussion

Characterizing ant assemblages in river red gum floodplain forest

The diversity of ground-foraging ants was found to be relatively low in river red gum floodplain forest with 41 morphospecies recorded in a total catch of 42 965 individuals.

Differences in methodology and sampling effort often make comparisons of diversity between studies difficult. Andersen (1983) recorded 71 species in a 50 m \times 25 m area of mallee, north-west of the current study area. (Mallee is a type of open eucalypt woodland that occurs in harsh, semi-arid areas of southern Australia.) Meeson *et al.* (2002) recorded 35 species of ant in pitfall traps in river red gum forest and surrounding farmland with a sampling effort less than 5% of the current study. Diversity in that study was boosted by open-area specialists inhabiting agricultural land; such species were not present in the forested areas sampled in the current study.

Did flooding increase assemblage variability or induce a quasi-equilibrial state?

Several studies have contended that flood perturbation induces a quasi-equilibrial state in the biota (e.g. Décamps 1993; Molles *et al.* 1998). However, definitions of what constitutes this equilibrium are not stated clearly, making testing of this idea difficult. In contrast, Oberdorff *et al.* (2001) considered increasing environmental variability, such as that created by flooding, to produce greater assemblage variability. Oberdorff *et al.* (2001) included explicit faunal-variability parameters in their hypotheses. Oberdorff *et al.* (2001) hypothesized that increased environmental variability reduces species richness, increases species turnover and increases compositional variation. In the current study, the species richness of ants decreased with increasing length of inundation during the 2000–2001 flood (Table 5.4, Fig. 5.2). Other studies also have shown that flooding is associated with reduced diversity in ground-foraging ants (Wilson 1987; Majer and Delabie 1994; Milford 1999). In additional, temporal compositional change in ant assemblages was positively correlated with flood duration (Fig. 5.3) (square-root transformed data), suggesting that flooding increased faunal variability.

However, the highest species turnover, considered indicative of the greatest faunal variability, occurred at the least flood-affected sites (Table 5.5). The results from repeating the analysis of compositional change with presence-absence data suggested that changes in the relative abundance of species, rather than the species present, were responsible for the large temporal variation in assemblage structure observed at the

flood-affected sites. Samways (1990) found that more species-rich ant assemblages had higher species turnover and thus, that increased diversity does not stabilize assemblages. Low species turnover and high compositional change is likely to occur whenever a perturbation-prone habitat is occupied by species, such as social insects, that experience large fluctuations in population size, but are persistent overall. The size of ant colonies may be reduced substantially by flooding, but the nest persists as long as reproductive individuals survive (Chapter Six).

Comparison of assemblage composition at recently emersed sites between 2001 and 2003 revealed consistency in the short-term assemblage structure associated with flooding. Soon after the recession of floodwaters, the composition of ant assemblages at sites that flooded a second time in 2002–2003 was not different from the January 2001 assemblage structure at the sites that experienced extensive flooding in 2000–2001 (Table 5.7). It was puzzling that the relatively brief flooding in 2002–2003 produced the same assemblage structure as extended flooding in 2000–2001. The assemblage structure at sites that flooded in 2002–2003 was expected to more closely resemble that at sites which flooded for only a moderate time in 2000–2001. Possibly, flood duration and frequency each influence the fauna. Thus, the response of ant assemblages to flooding did not accord entirely with either increased variability or attainment of a quasi-equilibrial state.

Influence of flooding on abiotic and biotic regulation

In the current study, differences in abundance, species richness and assemblage composition of ants between sites existed before the 2000–2001 flood. This made it impossible to definitively attribute the differences to flooding, but suggests that long-term effects of flooding on habitat might regulate ant assemblages. Flooding produces a denser tree canopy and increases production of leaf litter (Stone and Bacon 1995), creating a more closed habitat. Habitat features that decrease insolation reduce ant activity (Brian and Brian 1951). However, river red gum forests are characterized as relatively open habitat, so that insolation might not be an important factor.

Flooding does not appear to 'release' ant assemblages from biotic regulation in the form of competition. Competitive Dominant Dolichoderinae formed the largest component of the ant fauna at all sampling times except May 2000, when Opportunists dominated. Moreover, longer inundation was associated with Dominant Dolichoderinae forming a greater component of the fauna (Table 5.9). One species, *Iridomyrmex* sp. (*mattiroloi* gp), comprised virtually all of the Dominant Dolichoderinae. Andersen (1995) observed that species-poor communities overwhelmingly were dominated by Dominant Dolichoderinae at heavily disturbed (urbanized) sites. Thus, competitive *Iridomyrmex* species appear to be able to maintain, and even enhance, their numerical dominance of ant assemblages in the face of a disturbance that does not produce a more open, insolated habitat. However, Opportunists formed a major element of the fauna at both flood-affected and drier sites (Fig. 5.5a and b). Thus, competition may not be sufficiently intense to exclude poor competitors.

The Opportunist *Rhytidoponera metailica* (Smith) comprised approximately 8% of the composite ant catch in the present study. *R. metallica* is renowned as a successful colonizer of disturbed habitats (Andersen and McKaige 1987; Hoffman and Andersen 2003), particularly across the dry inland of southern Australia (Brown and Wilson 1956). In most species of *Rhytidoponera*, reproductively functional workers have taken the place of winged queens, making aerial dispersal of female nest founders impossible. *R. metallica* is the only species from this genus known to retain occasional queen

production (Ward 1986). No other species of *Rhytidoponera* was captured in this study. Plasticity of life-history traits may account for the ability of *R. metallica* to quickly recolonize areas following flooding.

In addition to flood-associated changes, the composition of ant assemblages differed with seasons, probably as a result of differential responses of species to ambient temperature change. The Dominant Dolichoderinae component of the fauna increased in the warmer spring/summer months at the expense of Opportunists, which simultaneously decreased (Table 5.9 and 5.11). This increase might be expected given that *Iridomyrmex* favours warmer habitats. Andersen (1986; 1995) recorded seasonal changes in the functional-group structure of ant assemblages in mesic southern Victoria, but found seasonal changes to be less marked in north-western Victoria—a result attributed to the milder winters in the semi-arid zone. Here, the seasonal changes in relative abundance of various functional groups, with different sensitivities to flooding, might explain why ANOSIMs did not reveal consistent structural differences between assemblages subject to different durations of flooding.

Ant predators (zodariid spiders) were relatively more abundant on drier sites compared to sites that were inundated for a moderate or extended period, even 2 yr after flooding (Table 5.13 and 5.14, Fig. 5.6). Thus, flooding potentially disrupts regulation of ant fauna by predation. That predation intensity, but not competition, was likely to have been reduced by flooding suggests that different biotic regulatory processes are disrupted by disturbance to varying extents. Intensity of competition appears to be less affected by flood disturbance than predation and thus, might contribute more to maintenance of assemblage structure within disturbance-prone habitats.

In conclusion, flood perturbation appears to reduce species turnover for ants. Prolonged or regular flooding allows only species that are resilient to flooding to persist. Because these species are able to cope with flooding biotic interactions (competition) between the resilient species can persist, even when disturbance disrupts biotic regulation imposed by less flood-tolerant species (predation). Therefore, disturbance does not necessarily result in suspension or reduction of biotic regulation. Flooding was associated with increased temporal variation in the relative abundance of species comprising assemblages. Ultimately, whether flooding is considered disruptive or stabilizing is contingent upon the relative importance given to abundance and persistence and, therefore, is subjective. However, the extent to which the perturbation response of social insects reflects that of species with different life-history characteristics is unknown.

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Functional Dominant Subordinate Opportunists Cold Climate Specialists Hot Climate Generalized Specia Group Dolichoderinae Camponotini (DD) (DD)	1 0010 0.								
Group Dolichoderinae Camponotini Specialists Myrmicinae Predat (DD)	Functional	Dominant	Subordinate	Opportunists	Cold Climate Specialists	Hot Climate	Generalized	Specialist	Cryptic Specie
(QQ)	Group	Dolichoderinae	Camponotini			Specialists	Myrmicinae	Predators	
		(DD)							
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traits	aggressive,	abundance,	poorty	sites where DD are	mennopunc	couldry, icas		INTABC IN SUIT
	good	competitively	competitive	less abundant	foraging	active and	population	and litter
	competitors	submissive to			behaviour to	aggressive	densities	
		DD			reduce	than DD		
					competition			
					with DD			
Most	Iridomyrmex	Camponotus,	Rhytidoponera	Stigmacros	Melophorus,	Pheidole,	Cerapachys	Rarely
common		Polyrachis	Paratrechina		Monomorium,	Crematogaster		caught in
genera in			¢		Meranopus			pitfall traps,
study								some
arca								Hypoponera
Parameter	Description	Mean ± SD	95% credible	Posterior				
------------------	--	---------------	--------------	------------------				
			interval	probability mass				
μ _{δΥ1}	Mean differences in abundance between flood treatments May 2000	0.40 ± 0.23	-0.07, 0.86	0.96*				
	(8 mo before flood)							
μ _{δY2}	Mean differences in abundance between flood treatments August 2000	0.38 ± 0.23	-0.08, 0.83	0.95*				
	(5 mo before flood)							

Table 5.3. Bayesian analysis of mean differences in ant abundances between flood treatments at each survey time.

Table 5.2. Critical parameter details for the Bayesian analysis of ant abundance.#

1999 B

0110 2742, 610 0116 -2.65, -2.03	nter sampling -2.34 ± 906ing 5.80 ±	ه Coefficient for autumn/win ها Coefficient for brief/no flo ها ما
91.9 ,24.2 61.0	±08.2 gniboo	الأمان المنافعة المنافع
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42.2,00.4 81.0	± 22.2 ±. gnibool	by Coefficient for extended fl
\$0.0 ,070 - 12.0	± de.0- gaibooft on	A-A Moderate flooding – brief
0.24 -1.04, -0.06	± 82.0- gnibooft on	P3-P3 Extended flooding – brief
72.0 ,76.0- 52.0	± 22.0- gnibooli ətsı:	b ₃ -b ₂ Extended flooding – mode
	0.16 4.90, 5.54 0.16 4.90, 5.54 0.121 -0.79, 0.05 0.23 -0.67, 0.27 0.23 -0.67, 0.27	0010g 5.44 ± 0.18 5.0, 5.54 0001ng 5.22 ± 0.16 4.90, 5.54 0001ng -0.36 ± 0.21 -0.79, 0.05 001000 -0.58 ± 0.24 -1.04, -0.06 001000 -0.52 ± 0.23 -0.67, 0.27 100100 -0.22 ± 0.23 -0.67, 0.27

t

* Data natural log transformed

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

Mean differences in abundance between flood treatments January 2001	0.58 ± 0.15	0.18, 0.80	1.00*
(immediately after flood)			
Mean differences in abundance between flood treatments May 2001	0.82 ± 0.24	0.25, 1.08	1.00*
(4 mo after flood)			
Mean differences in abundance between flood treatments August 2001	1.06 ± 0.35	0.31, 1.39	1.00*
(7 mo after flood)			
Mean differences in abundance between flood treatments November 2001	0.11 ± 0.19	-0.13, 0.57	0.61
(10 mo after flood)			
Mean differences in abundance between flood treatments January 2002	-0.05 ± 0.26	-0.32, 0.55	0.32
(12 mo after flood)	I		
Mean differences in abundance between flood treatments November 2002	-0.10 ± 0.29	-0.46, 0.54	0.31
(22 mo after flood)			
Mean differences in abundance between flood treatments January 2003	0.42 ± 0.14	0.12, 0.71	0.99*
(24 mo after flood)			
	Mean differences in abundance between flood treatments January 2001 (immediately after flood) Mean differences in abundance between flood treatments May 2001 (4 mo after flood) Mean differences in abundance between flood treatments August 2001 (7 mo after flood) Mean differences in abundance between flood treatments November 2001 (10 mo after flood) Mean differences in abundance between flood treatments January 2002 (12 mo after flood) Mean differences in abundance between flood treatments November 2002 (22 mo after flood) Mean differences in abundance between flood treatments November 2002 (22 mo after flood) Mean differences in abundance between flood treatments November 2002 (22 mo after flood)	Mean differences in abundance between flood treatments January 2001 0.58 ± 0.15 (immediately after flood) 0.82 ± 0.24 Mean differences in abundance between flood treatments May 2001 0.82 ± 0.24 (4 mo after flood) 1.06 ± 0.35 (7 mo after flood) 1.06 ± 0.35 (7 mo after flood) 0.11 ± 0.19 (10 mo after flood) 0.11 ± 0.19 (12 mo after flood) -0.05 ± 0.26 Mean differences in abundance between flood treatments January 2002 -0.05 ± 0.26 (12 mo after flood) -0.05 ± 0.26 Mean differences in abundance between flood treatments November 2002 -0.10 ± 0.29 (22 mo after flood) -0.10 ± 0.29 Mean differences in abundance between flood treatments January 2003 0.42 ± 0.14 (24 mo after flood) -0.25 ± 0.26	Mean differences in abundance between flood treatments January 2001 0.58 ± 0.15 $0.18, 0.80$ (immediately after flood)Mean differences in abundance between flood treatments May 2001 0.82 ± 0.24 $0.25, 1.08$ (4 mo after flood) 0.82 ± 0.24 $0.25, 1.08$ $(4 mo after flood)$ Mean differences in abundance between flood treatments August 2001 1.06 ± 0.35 $0.31, 1.39$ (7 mo after flood) 1.06 ± 0.35 $0.31, 1.39$ (7 mo after flood) 0.11 ± 0.19 $-0.13, 0.57$ (10 mo after flood) 0.05 ± 0.26 $-0.32, 0.55$ (12 mo after flood) 0.05 ± 0.26 $-0.32, 0.55$ (12 mo after flood) 0.10 ± 0.29 $-0.46, 0.54$ (22 mo after flood) 0.42 ± 0.14 $0.12, 0.71$ (24 mo after flood) 0.42 ± 0.14 $0.12, 0.71$

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

.ognage.	leitnetedus a	pe (of bemeal	differences, c	ior negative	$01.0 \ge 10.00.05$ *

*01	1.84, 2, 13	2010 + 861	Sources and the sources of the sourc	۲ <u>۶</u>
*0'l	1.84, 2.13	70.0 ± 80.1	Coefficient for medium flooding	^z d
*0°1	1.62, 1.90	70.0 ± 67.1	Coefficient for extended flooding	ig Id
*0	01.0- ,74.0-	01.0 ± 92.0-	Moderate flooding – brief/no flooding	ig-zg 5-1
•0	25.0- ,17.0-	01°0∓15°0-	Extended flooding – brief/no flooding	lQ-EQ
•0	£0 . 0- ,04.0-	-0.22 ± 0.10	Extended flooding – moderate flooding	^z g-&g

Table 5.4. Critical parameter details for the Bayesian analysis of species richness of ants.

Table 5.5. Critical parameter details for the Bayesian analysis of species turnover of ants.	

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
β_l	Coefficient for brief/no flooding	0.23 ± 0.03	0.17, 0.30	1.0*
β_2	Coefficient for medium flooding	0.14 ± 0.03	0.08, 0.21	1.0*
β_3	Coefficient for extended flooding	0.17 ± 0.03	0.11, 0.23	1.0*
β_2 - β_1	Moderate flooding – brief/no flooding	$\textbf{-0.09} \pm 0.04$	-0.17, -0.01	0.02*
β_3 - β_1	Extended flooding – brief/no flooding	-0.07 ± 0.04	-0.15, 0.02	0.06*
β_{3} - β_{2}	Extended flooding – moderate flooding	0.02 ± 0.04	-0.06, 0.10	0.76

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

1

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
µฮา <i>เ</i>	Mean differences in species turnover between flood treatments	0.03 ± 0.02	0.0.08	0.97*
	January 2001-2002	0.05 ± 0.02	0, 0.00	0.27
μδγ2	Mean differences in species turnover between flood treatments	0.05 ± 0.02	0.01.0.09	0.00*
	January 2002–2003	0.03 ± 0.02	0.01, 0.09	0.99

Table 5.6. Bayesian analysis of mean differences in species turnover of ants between flood treatments, January 2001-2002 and 2002-2003

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

Sampling time	Mont hs since flood	Total ants trapped to characterize assemblage	Extended flooding vs. brief/no flooding			Modera floodin	Moderate flooding vs. brief/no Extended flooding vs. flooding moderate flooding)			Extended flooding vs. moderate flooding	
			R	<i>P</i> -	Permutations	R	<i>P</i> -	Permutations	R	P-	Permutations
May 2000	Pre-	686	0.620	value 0.008	126	-0.008	value 0.489	462	0.517	0.006	462
	flood	(16 sites)									
	(-8)										
August	Pre-	170	0.006	0.425	126	0.131	0.267	462	0.214	0.100	210
2000	flood	(16 sites)				i i					
	(-5)					ļ					
January	0	10 035	0.503	<0.001	11 440	0.257	0.011	6435	0.256	0.007	20 000
2001											
May 2001	4	2076	0.250	0.015	11440	0.130	0.076	6435	0.103	0.099	20 000
August		1167	0.272	0.013	6435	0.441	0.005	1716	-	0.473	6435
2001			Ì						0.017		
November	10	4346	0.460	<0.001	11 440	0.066	0.168	6435	0.118	0.070	20 000
2001	ļ										
January	12	13 266	0.581	<0.001	11 440	0.205	0.009	6435	0.199	0.026	20 000
2002											
November	22	5959	0.242	0.003	6435	0.020	0.328	1716	0.385	0.003	3003
2002		(21 sites)									
January	24	[•] 4194	0.338	0.002	6435	-0.045	0.617	792	0.234	0.042	1287
2003		(20 sites)									
<u></u>	•					<u> </u>	··- ···		- <u></u>	· · ·	

Table 5.8. Analysis of similarities results for ant assemblages sampled before and over a 2-yr period after flooding in 2000–2001 (excludes sites that re-flooded in 2002–2003).

Table 5.7. Analysis of similarities results for comparison of ant assemblages at recently flooded sites in January 2003 with recently flooded sites in January 2001.

	in 3 years			
Recent brief/no flooding	Recently flooded for 2^{nd} time	£6S.0	900.0	330
	in 3 years			
gnibooft starsbom tassaS	Recently flooded for 2 nd time	904.0	210.0	564
	in 3 years			
Recent extensive flooding	Recently flooded for 2 nd time	691'0-	£88.0	S1 <i>L</i>
			ənjex	
Plood history at sampling time	Plood history at sampling time	R	~d	Permutations
January 2001	January 2003			

leemed to be a substantial change.	* ≥ 0.90 or ≤ 0.10 for negative differences,
------------------------------------	--

zd-ed	Extended flooding – moderate flooding	80.0 ± 61.0	9:0 't0'0	*65'0
id-&d	gniboolt on\torid - gniboolt bobnotxH	60.0 ± 22.0	0.0, 0,0,0	*66'0
Id-Id	Moderate flooding – briet/no flooding	60.0 ± €0.0	17:0 1/1:0-	¢0,0
٤ď	Coefficient for extended flooding	90°0 ∓ <i>L</i> 8°0	66'0 '9/'0	-0°1
ت ا¢ت	Coefficient for medium Hooding	90.0 ∓ \.9.0	0.56, 0.00	*0.1
- !d	Coefficient for briel/no flooding	10.0 ± 40.0	81.0 ,046.0	*0 1
σ α	Coefficient for autumn/winter sampling	CU.U I CC.U-	67'0+ ⁽ ++'0+	*01
rarameter	ມດາຊຸມ	UC I RESIM		
Tatamered	Description	02 ± 000	Invratni aldiharo %29	Posterior probability mass

Table 5.9. Critical parameter details for the Bayesian analysis of Dominant Dolichoderinae as a proportion of total ant fauna.

Table 5.10. Bayesian analysis of mean differences in proportion of Do	ominant Dolichoderinae between flood treatments at each survey	¹ time.
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Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
μ _{σγ1}	Mean differences in abundance between flood treatments May 2000	$\textbf{-0.10} \pm \textbf{0.08}$	-0.25, 0.04	0.08*
	(8 mo before flood)			
μ _{sr2}	Mean differences in abundance between flood treatments August 2000	-0.06 ± 0.08	-0.21, -0.06	0.23
	(5 mo before flood)			
μ _{δΥ3}	Mean differences in abundance between flood treatments January 2001	-0.17 ± 0.04	-0.25, -0.08	0.00*
	(immediately after flood)			
µsy4	Mean differences in abundance between flood treatments May 2001	-0.06 ± 0.04	-0.16, 0.01	0.05*
	(4 mo after flood)			
<i>µs</i> rs	Mean differences in abundance between flood treatments August 2001	-0.12 ± 0.05	-0.21, -0.02	0.01*
	(7 mo after flood)			
μ5γ6	Mean differences in abundance between flood treatments November 2001	-0.25 ± 0.04	-0.32, -0.14	0.00*
	(10 mo after flood)			
µsrī	Mean differences in abundance between flood treatments January 2002	-0.14 ± 0.04	-0.23, -0.06	0.00*
	(12 mo after flood)			
µsrs	Mean differences in abundance between flood treatments November 2002	-0.21 ± 0.05	-0.30, -0.10	0.00*
· ·	(22 mo after flood)			
μ _{δΥ9}	Mean differences in abundance between flood treatments January 2003	-0.12 ± 0.05	-0.21, -0.03	0.01*
	(24 mo after flood)			

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

.

Parameter	Description	Mean±SD	95% credible	Posterior probability
			interval	ssem
11877	Mean differences in abundance between flood treatments May 2000	<u>70.0 ± 20.0</u>	-0.12, 0.15	09'0
·	(8 mo before flood)			
<i>₹.\9</i> 71	0002 nuguA stromtest hooft noowtod sonchuds in soonstaftib meaM	L0.0 ± 40.0-	-01.0,81.0-	72.0
	(5 mo before flood)			
EX871	Mean differences in abundance between flood treatments January 2001	1 0.0±0	80.0 ,60.0-	\$\$.0
	(immediately after flood)			
\$19tf	Mean differences in abundance between flood treatments May 2001	40.0 ± 11.0 -	0 '61'0-	*20.0
	(4 mo after flood)			
5 <i>19</i> 71	Mean differences in abundance between flood treatments August 2001	90'0 ∓ <i>L</i> 1'0-	to:0- '92:0-	*10.0
	(7 mo after flood)			
918 ₁₁	Mean differences in abundance between flood treatments November 2001	20.0 ± 40.0-	21.0 , 70.0-	28.0
	(10 mo after flood)			
41971	Mean differences in abundance between flood treatments lanuary 2002	40.0 ± 80.0-	-0.16, 0.02	*10.0
	(12 mo after flood)			
878 L	Mean differences in abundance between flood treatments November 2002	20.0 ± 40.0	£1.0 ,80.0-	08.0
	(22 mo after flood)			
61871	Mean differences in abundance between flood treatments lanuary 2003	20.0 ± 80.0-	20.0 ,81.0-	*10.0
	(24 mo atter flood)			

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

Table 5.12. Bayesian analysis of mean differences in proportion of Opportunists between flood treatments at each survey time.

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Table 5.11. Critical parameter details for the Bayesian analysis of Opportunists as a proportion of total ant fauna.

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
α	Coefficient for autumn/winter sampling	0.33 ± 0.04	0.24, 0.41	1.0*
βι	Coefficient for brief/no flooding	0.13 ± 0.06	-0.01, 0.25	1.0*
β_2	Coefficient for medium flooding	0.26 ± 0.06	0.15, 0.38	1.0*
R.	Coefficient for extended flooding	0.22 ± 0.06	0.11. 0.34	1.0*

β2-βI	Moderate flooding – brief/no flooding	0.13 ± 0.08	-0.04, 0.30	0.94*
β_{3} - β_{1}	Extended flooding - brief/no flooding	0.09 ± 0.08	-0.07, 0.26	0.86
β_3 - β_2	Extended flooding – moderate flooding	-0.04 ± 0.07	-0.19, 0.10	0.30

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

Table 5.13. Critical parameter details for the Bayesian analysis of the ratio of ants to ant-eating spider (Zodariidae) abundance # in relation to flood duration.

Parameter	Description	Mean ± SD	95% credible interval	Posterior probability mass
β_l	Coefficient for brief/no flooding	4.20 ± 0.26	3.66, 4.74	1.0*
β_2	Coefficient for medium flooding	5.04 ± 0.23	4.60, 5.48	1.0*
β_3	Coefficient for extended flooding	5.05 ± 0.21	4.61, 5.46	1.0*

January 2003 EX971 0 '98'0-22.0 ± 64.0-Mean difference in ants/zodariids ratio between flood treatments *20.0 S002 Vieunel 7,877 -0.65 ± 0.20 Mean difference in ants/zodariids ratio between flood treatments 22.0- ,70.1-*0 January 2001 1784 Mean difference in ants/zodariids ratio between flood treatments 81.0- ,52.0-81.0 ± 82.0-*****0 probability mass Interval Parameter Description 95% credible $Mean\pm SD$ Posterior January survey.

Table 5.14. Bayesian analysis of mean differences in the ratio of ants to ant-eating spiders (Zodariidae)" between flood treatments for each

* Data natural log transformed

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.

$\beta_2 - \beta_1$	Moderate Hooding – brief/no Hooding	0.83 ± 0.33	0.17, 1.51	0.99%
β3-β1	Extended flooding – brief/no flooding	0.84 ± 0.34	0.15, 1.52	0.99*
β_{3} - β_{2}	Extended flooding – moderate flooding	0.01 ± 0.33	-0.64, 0.70	0.52

[#]Data natural log transformed

* ≥ 0.90 or ≤ 0.10 for negative differences, deemed to be a substantial change.



different durations and frequency of inundation.



Figure 5.2. Mean species richness (± SE) of ground-active ants over time at sites subject to different durations and frequency of inundation.

Figure 5.1. Mean abundance (\pm SE) of ground-active ants over time at sites subject to



Figure 5.3. Relationship between variability in the composition of ant assemblages (R-statistic) over two years (2001-2002, 2002-2003) and duration of flooding in 2000-2001 (1= no or brief flooding, 2 = moderate flooding, 3 = extended flooding) $(r^2 = 0.80, P \approx 0.016).$



Figure 5.4. Percentage of ant assemblages comprised by major genera on sites that experienced (a) extended flooding in 2000-2001; (b) brief or no flooding in 2000-2001.





















Figure 5.5. Percentage of ant assemblages comprised by major functional groups on sites that experienced (a) extended flooding in 2000-2001; (b) brief or no flooding in 2000-2001.

May 01 Aug. 01 Nov, 01 Jan, 02 Nov. 02 Jan. 03 1,#



Appendix 5.1. Species of Formicidae (Hymenoptera) pitfall trapped or trapped on tree trunks (Chapter Six) and their functional groups (DD = Dominant Dolichoderinae, SC = Subordinate Camponotini, O = Opportunist, CC = Cold Climate Specialist, HC = Hot Climate Specialist, GM = Generalized Myrmicinae, SP = Specialist Predator, CS = Cryptic Species. (Ref. no. refers to a reference number used to identify morphospecies in the voucher collection.)

Cerapachyinae Cerapachys sp.1

Dolichoderinae

Species

Doleromyrma sp.1 (darwiniana gp) Iridomyrmex sp.1 (mattiroloi gp) Iridomyrmex sp.2 (purpureus gp) Iridomyrmex sp.3 (pallidus gp) Iridomyrmex sp.4 Iridomyrmex sp.5 Ochetellus sp.1 (glaber gp) Ochetellus sp.2 Tapinoma sp.1 (minutum gp)

Formicinae

Camponotus aeneopilosus Mayr Camponotus sp.1 (nr. consobrinus) Camponotus sp.2 (claripes gp) Camponotus sp.3 (gasseri gp) Camponotus sp.4 Camponotus sp.5 (fictor gp)

 Refno	Functional	Present on the	Present on
	group	forest floor	tree trunks
40	SP	1	
184	0	1	
4	סח		5
11	סס		-
14	סס		
43	DD	- -	1
46	סס		1
10	о <i>р</i> У		
47	?	1	1
188	0	1	1
100	Ŭ	-	
6	SC	√	√
l	SC	1	1
1A	SC	1	1
32	SC	1	√
35/35b	SC	1	√
37	SC		√

Appendix 5.1. continued

Species	Refno	Functional	Present on the	Present on
		group	forest floor	tree trunks
Melophorus sp.1 (mjobergi gp)	23A/23B	HC	1	V
Melophorus sp.2	39/42	HC	1	
Melophorus sp.3	53	HC	1	
Notoncus sp.1	41	CC	4	
Notoncus sp.2	52	CC	√	
Paratrechina sp.1 (obscura gp)	2	0	1	√ (rarely)
Polyrhachis phryne Forel	5	SC	4	√
Polyrhachis sp.1 (sidnica gp)	5B	SC	1	1
Polyrhachis sp.2	48	SC		√ (singleton)
Polyrhachis sp.3	55	SC		√ (singleton)
Stigmacros sp.1 (intacta gp)	7	CC	1	
Stigmacros sp.2	38/44	CC	√ ;	
Myrmeciinae				
Myrmecia sp. 1	21	SP	1	
Myrmicinae				
Crematogaster sp.1 (laeviceps gp)	16	GM	1	√
Meranoplus sp.1	9	HC	1	
Meranoplus sp.2	9	HC	1	
Meranoplus sp.3	50	HC	1	
Monomorium sp.1(laeve gp)	13	HC	1	
Monomorium sp.2 (rothsteini gp)	27	HC	1	
Monomorium sp.3	27B	HC	1	
Monomorium sp.4	27C	HC	1	
Pheidole sp.1 (Group D)	8B	GM	1	
Pheidole sp.2 (Group D)	8B	GM	1	
Podomyrma gratiosa (Smith)	22	CC	1	√
Podomyrma adelaidae Forel	26	CC	1	√
Podomyrma (?)ferruginea (Clark)	36	CC		√

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Appendix 5.1. continued

Species

5

Podomyrma sp.1 (elongata gp) Podomyrma sp.2 Podomyrma sp.3

Ponerine Hypoponera sp.1 Rhytidoponera metallica (Smith)

•

Ref no	Functional	Present on the	Present on tree
	group	forest floor	trunks
 31	CC	1	
34	CC	1	1
17	CC		\$
12	CS	✓ ¹	
3	0	1	✓ (rarely)

CHAPTER SIX .

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USE OF TREES AS REFUGIA BY FLIGHTLESS TERRESTRIAL INVERTEBRATES DURING FLOODING IN RIVER RED GUM EUCALYPTUS CAMALDULENSIS FOREST

Abstract

Use of arboreal flood refugia by spiders and ants was investigated in river red gum Eucalyptus camaldulensis floodplain forest to determine whether (1) trunk ascent is a widely used flood-survival strategy; (2) species that are routinely active on both tree trunks and the forest-floor have a flood-survival advantage over exclusively ground-active species; and (3) flood effects propagate into the arboreal strata, affecting exclusively arboreal species. Ground-nesting ants continued to be active on tree trunks standing in floodwaters, suggesting that these species were able to utilize arboreal flood refugia. The species richness of ground-nesting ants that utilized arboreal refugia did not decline on the forest floor following flooding. However, while the use of refugia enabled certain species of ground-nesting ants to persist in flood-prone areas, it did not protect against floodassociated declines in abundance. In contrast, few ground-active spiders moved into trees in response to flooding. The abundance and species richness of spiders did not decline on the forest floor following flooding, suggesting that flood-survival strategies other than trunk ascent were used successfully or floodplain spider assemblages. However, semiarboreal spiders comprised nearly half of the spiders caught on the forest floor. Neither the abundance nor species richness of exclusively arboreal taxa changed in response to flooding. The composition of spider and ant assemblages on tree trunks differed between areas subject to prolonged flooding of the forest floor compared with drier areas. Therefore, propagation of flood effects into the arboreal fauna was slight. The use of arboreal flood refugia in river red gum forest appears limited to a few species, but this strategy might be central to the persistence of large populations of those species on the floodplain.

Introduction

Floodplains are dynamic environments that alternate between a terrestrial and an aquatic phase (Junk 1997). In their model of floodplain ecology, the Flood Pulse Concept, Junk et al. (1989) contended that habitats within floodplains shift horizontally or vertically, depending on the water level. They considered the floodplain-forest canopy to be a "terrestrial" habitat, harbouring an "abundance" of animals capable of re-colonizing floodaffected areas (Junk et al. 1989). The Flood Pulse Concept was developed largely using Amazonian floodplain forest, where flood patterns are ancient and highly predictable, as an exemplar. Invertebrates that are active on the ground during the dry phase in Amazonian floodplain forests migrate into tree canopies before flooding commences, in response to proximate environmental cues (Adis 1984; Adis and Junk 2002). The level of complexity and specificity of flood-survival adaptations in invertebrates is considered to be contingent upon the predictability and history of the flood regime (Adis and Junk 2002). Therefore, ground-active invertebrates in floodplain forests where flood patterns are less ancient and less predictable than in Amazonia might not experience the canopy as an alternative "terrestrial" habitat. Adis and Junk (2002) reported that terrestrial invertebrates on European floodplains also move into arboreal refugia, but cited no data to support their claim.

Understanding the prevalence of particular flood-survival strategies is important to developing general models of floodplain ecology. In Australia, riparian floodplain forests consist of pure stands of river red gum *Eucalyptus camaldulensis* Denhn.. The forest floor frequently is inundated for extended periods of time. The bark of river red gum forms large, loose sheets that provide a humidity-regulated microhabitat. Hence, the trunks and canopies of river red gums might provide flood refugia for flightless invertebrates that are active on the forest floor during dry periods. However, river red gums support a rich, specialized, subcortical fauna (Baehr 1990). The subcortical fauna is characterized by high numbers of predatory species, such as sparassid and clubionid spiders and carabid beetles (Baehr 1990). This might create a situation where normally ground-dwelling species

seeking arboreal refugia have to 'run the gauntlet' of competition and/or predation by subcortical species on the lower trunk. Under such conditions, trees might be perceived as hostile environments rather than valuable flood refugia. As an alternative to climbing trees, ground-dwelling species might employ a 'risk strategy,' whereby they breed and recolonize during dry periods and experience catastrophic population declines, at a local scale, when floods occur (Adis and Junk 2002). Alternatively, horizontal movement away from floodwaters might be the prevalent flood-survival strategy among the more mobile taxa.

In the current study, I investigated use of arboreal refugia by flightless invertebrates in Barmah Forest—a river red gum floodplain forest. In geological time, the floodplain forest was formed recently; Barmah Forest is estimated to be only 10 000-13 000 yr old (Bowler and Harford 1966). River regulation in the last 70 yr has increased variability in the timing and extent of flooding, although the extent of flooding naturally varied between years (Bren et al. 1987). Thus, flood regimes are neither ancient nor highly predictable and flightless invertebrates might be expected to behave opportunistically in response to flooding. Spiders and ants were sampled on tree trunks and on the forest floor to determine if each habitat supported a distinct fauna. The flood response of the fauna active only on tree trunks, only on the forest floor and on both trunks and the ground was examined to determine whether habitat-use characteristics are linked to flood tolerance. The extent to which usually ground-active species seek refuge in trees, and how this behaviour affects subcortical fauna, was assessed. Spiders and ants were sampled on the forest-floor after flooding to determine whether use of arboreal refugia facilitated numerical dominance of forest-floor fauna. An examination of distributional patterns in species not found to use arboreal refugia was used to infer the efficacy of the 'risk strategy' for persisting on the floodplain. Last, the flood responses of several abundant species were considered individually to assess the level of idiosyncrasy in flood reponses between related species.

Methods

Study area

This study was conducted in Barmah State Forest and Barmah State Park on the Murray-River floodplain, in northern Victoria, Australia (35°55'S 145°08'E). Barmah Forest covers 29 500 ha and consists largely of monospecific stands of Eucalyptus camaldulensis with an understorey of grasses, sedges and rushes (Chesterfield 1986). Spiders and ants were collected on the ground with pitfall traps and collected on tree trunks with skirt traps -a type of photo-eclector.

Skirt-trap design and sampling protocol

Invertebrates ascending tree trunks were sampled with skirt traps. The trap design is a modification of Funke's arboreal photo-eclector (Funke 1971). Whereas Funke's design necessitates several photo-eclector traps to circumscibe the trunk, a single skirt trap per tree is sufficient to collect invertebrates ascending the trunk.

The trap consisted of a black, fabric skirt wrapped around the trunk with an inside diameter ≈ 0.30 m and an outside diameter ≈ 1 m (Fig. 6.1). Elastic around the inner diameter of the skirt kept the 'waist' flush with the bark on the trunk and allowed for variation in trunk size. A hoop of 10 mm-diameter polypropylene pipe was sewn into the hem of the skirt to impart rigidity. The hoop and four guy ropes held the skirt away from the trunk, thereby creating a barrier to the upward movements of invertebrates.

A transparent, plastic collecting jar was attached to the skirt close to the trunk. Invertebrates encountering the barrier to upward movement travelled around the trunk until they reached the hole in the skirt, which opened into the collecting jar. The invertebrates

phototaxied into the collecting jar. The collecting jar contained a moat of preserving solution of 25% glycerol: 55% propanol: 20% water. The preservative might have attracted some invertebrates to the trap, but it is unlikely to have been a powerful attractant of ants (Greenslade and Greenslade 1971). The collecting jar was secured to the trunk with an aluminum bracket and a nail. Guy ropes attached to adjacent trees prevented movement of the skirt trap in strong wind. A piece of 10 mm² metal mesh placed in the entrance of the collecting jar prevented small vertebrates entering the trap.

Five skirt traps were put on river red gum trees at each of four sites throughout Barmah Forest: Buck's Lake (high flood-proneness), Rat Castle Creek (moderate flood-proneness), Opposite Buck's Sandhill (moderate flood-proneness) and Near Dharnya (low flood-proneness). Traps were positioned ca 2 m above ground level. The traps were in position for 3 mo, from early October to early January, during both 2001–2002 and 2002–2003. Each month, traps were cleared and moved to other trees within the study sites. Buck's Lake was the only site to be flooded during the 2001–2002 sampling period. It was briefly inundated in October 2001, and again in November 2001; floodwaters receded by December 2001. Buck's Lake and Rat Castle Creek were flooded during October and November 2002. The forest floor at Opposite Buck's Sandhill was inundated only during November 2002. No sites were flooded for the entire December sampling period, although the ground at sites flooded in November remained muddy throughout December.

Pitfall-trapping protocol

Pitfall trapping was conducted at 24 50 m \times 50 m sites located throughout Barmah Forest in January 2001, January 2002 and January 2003. Five pitfall traps with an opening diameter of 75 mm and depth of 95 mm were set on each study site. For ease of re-location, the pitfall traps were spaced ca 2 m apart on a randomly positioned line within each study site. Traps were closed for \geq 24 h following installation to counter possible 'digging-in' disturbance effects (Greenslade 1973). Pitfall traps then were filled with a 70% propanol:

5% glycerol: 25% water solution and opened for five days and nights. The contents of the five traps were considered sub-samples and were pooled for each site.

In the austral spring/summer 2000–2001, Barmah Forest experienced widespread flooding. Floodwaters receded by January 2001. Because the duration of flooding at each study site was not measured directly, a *post facto* measure of inundation was devised. Study sites were rated as having experienced 'brief/no,' 'moderate' or 'extended' flooding based on the following suite of site characteristics:

(i) brief or no floo no aquatic-inse
(ii) moderate flood but may be son present, may be
(iii) extended flood pupal cases of deposition, 'wa

The duration of flooding occurring at each site could not be predicted when the sites were selected, so the study design was unbalanced with nine sites categorized as experiencing extended flooding, eight sites experiencing moderate flooding and the remaining seven sites were subject to brief or no flooding.

The following year, austral spring/summer 2001–2002, none of the pitfall-trap sites were inundated. The forest flooded to a lesser extent in spring/summer 2002–2003, with four pitfall-trap sites experiencing some level of flooding. Thus, four pitfall-trap sites flooded twice during the study period, thirteen sites flooded once and seven sites were not inundated at all.

brief or no flooding - soil dry and compacted, ground cover of dry grasses, no aquatic-insect pupal cases evident;

moderate flooding – soil dry, ground covering generally of verdant grass, but may be some dead, aquatic plants present, few aquatic-insect pupal cases present, may be some silt deposited by floodwaters evident;

extended flooding - damp soil, considerable growth of water plants, many pupal cases of aquatic insects attached to tree trunks, often extensive silt deposition, 'watermark' left on tree trunks.

Handling of samples

Samples from both pitfall and skirt traps were sieved (1 mm²) to remove fine debris and stored in a 70% ethanol: 30% distilled water preservative. Specimens were sorted to morphospecies. Only adult spiders were included in the analysis because (morpho)species-level identification was not possible for immature specimens. Ants were identified to genus. Presence of winged, reproductive ants in samples was noted, but winged individuals were excluded from further analyses because they have greater mobility than flightless castes. Moreover, their inclusion could have resulted in an over-estimation of diversity because reproductives often are morphologically dissimilar to workers. Spiders were identified to family or, where possible, genus. For those families where taxonomic expertise is available, expert assistance was sought to identify voucher specimens to species (see acknowledgements).

Data analysis

All analyses were performed separately for spiders and ants.

Species present in pitfall traps (ground-active) and skirt-traps (trunk-active) were compared and species were grouped by habitat use. The four groups identified were:

- (i) arboreal: species only active on trees;
- (ii) strictly terrestrial: species only active on the ground;

(iii) semi-arboreal: species always active on both the ground and in trees, including ground-nesting ants that forage on tree trunks;

(iv) 'refugees': species usually active only on the ground, found on tree-trunks only during flooding.

Forest-floor spiders and ants

Flood-related compositional changes in ground-active spider and ant assemblages are related in Chapters Four and Five.

The unpredictable and variable flood patterns that occurred during this project resulted in an unbalanced experimental design, preventing separate testing for the effects of flood duration and flood frequency. Although modelling the effects of flood frequency (i.e. the number of times a site flooded in the 3-yr study period) on ground-active fauna would synthesize the trunk data and forest-floor data better, such an analysis would be inconsistent with the rest of thesis. Therefore, I decided to focus on the influence of flood duration in the statistical analysis. However, sites that flooded twice during the study period are considered separately.

No summer before-data were available for the extensive spring/summer 2000–2001 flood. However, the January 2001 pitfall-trap data were stratified by duration of inundation (no/brief flooding, moderate flooding, extended flooding,) allowing a 'snapshot' comparison of forest-floor fauna between sites to be made at that time. Comparison of the abundance and species richness of taxa with different habitat-use patterns on sites exposed to varying durations of inundation was used to determine if species that use arboreal strata, as well as the forest floor, respond to flooding differently compared with species that only use the forest floor. The brief flooding of four study sites in spring 2002 allowed changes in the fauna over that period to be contrasted between flooded and unflooded sites. However, few sites were inundated and there was insufficient variation in the immersion period to permit the 2002–2003 data to be stratified by flood duration. Therefore, the 2002–2003 analysis is a flooded/unflooded comparison, rather than an attempt to measure a more graduated response to inundation period.

Flooding in spring 2002 was brief compared to spring/summer 2000-2001. The faunal changes associated with the 2002 floods were less marked than the changes associated with the 2000-2001 floods. This is likely to be a result of the brevity of the inundation period moderating its impact, combined with the earlier recession of flood waters providing more

time for flood-induced changes to attenuate before the January sampling period. In addition, 17 sites flooded in spring/summer 2000–2001 compared to four in 2002. Thus, the January 2001 pitfall-trap data have the potential to reveal flood responses not seen in the January 2003 data. One-factor (duration of inundation) ANOVAs were performed on the January 2001 data for each of the following dependent variables: abundance of total taxa, species richness of total taxa, abundance of semi-arboreal taxa, species richness of strictly terrestrial taxa.

To ascertain whether short-term flood tolerance is a function of habitat-utilization patterns, change in each of the following variables between January 2002 and January 2003 was calculated at the 17 flood-prone sites: abundance of total taxa, species richness of total taxa, abundance of semi-arboreal taxa, species richness of semi-arboreal taxa, abundance of strictly terrestrial taxa, species richness of strictly terrestrial taxa. T-tests were used to determine whether the mean change in each of the variables from January 2002 to January 2003 differed between sites that flooded and did not flood for a second time in spring 2002. The same test was used to examine influence of flooding on the abundance of the following taxa: Argoctenus 'samueli' sp. nov. Raven (manuscript name) (Araneae: Zoridae), Supunna picta (Koch) (Araneae: Corinnidae), three Camponotus species (large ground-nesting, trunk-active ant species), Iridomyrmex sp.(mattiroloi gp.) (small ground-nesting, trunkactive ant species) and *Rhytidoponera metallica* (Smith) (ground-active ant species). The rarity of 'refugees' (i.e. species that only are active on tree trunks during floods) precluded statistical analyses on those taxa. Only the 17 sites that flooded in spring/summer 2000-2001 were included in the analyses because these sites were assumed to be following similar successional trajectories, whereas the seven sites that never flooded/flooded very briefly might be following very different paths, introducing unwarranted variability into the analyses. Only the results of *t*-tests that were statistically significant at the 0.05 level are reported.

Tree-trunk spiders and ants

To determine whether flooding influenced the composition of faunal assemblages on treetrunks, Bray-Curtis similarity matrices were computed from species-by-site matrices using the PRIMER statistical package (Version 5, Clarke and Warwick 1994). The results presented are based on square-root-transformed data to moderate the influence of highly abundance species; however, a variety of transformations were tried and results were robust to the choice of transformation.

One-factor analysis of similarities (ANOSIM), using a maximum of 20 000 iterations, were performed on the matrices. Ideally, the data would have been divided into three groups according to stage in the flooding cycle: (1) flooded sites; (2) recently emersed sites; and (3) sites that had not flooded that year. However, replication was at the site level, so data from the five traps at each site were pooled for each month. This resulted in only four data points in the group of recently emersed sites. The low statistical power arising from the small sample size produced ambiguities in the ANOSIM, whereby the pairwise comparisions between groups produced almost identical *R*-values (average levels of faunal similarity), but the result was statistically significant only for the groups with larger sample sizes. After examination of the relevant non-metric, multidimensional scaling plots, the data were pooled into two groups: (1) sites that were flooded at the time of sampling sites or had flooded in the past two months and (2) sites that had not flooded for > 1 yr.

The skirt-trapping sampling design involved repeated measures of study sites, and thus, samples were not independent. ANOSIM cannot adjust probabilities accordingly and, consequently, all probabilities from these analyses should be considered underestimates of the actual probabilities. Similarity percentages (SIMPER) analyses were performed to identify species contributing most to differences in assemblages among sites.

Variation in faunal abundance between months prevented pooling of samples taken in different months. Furthermore, flooding cut access for 1 wk to two of the sites during late December 2002. This resulted in an uneven sampling effort between sites and months. To allow for uneven sampling effort, abundances of the different habitat-use groups were expressed as a proportion of total catch for each site. Analyzing data in this way did not change the findings for habitat-use groups and so, abundance results, rather than

proportions, are presented. However, the responses of single species are presented as proportional abundances to reduce variation created by the unequal sample sizes.

Because sample size was small (four sites × 2 yr data collection = eight samples for each month), it was not possible to know if the data were normally distributed. Consequently, non-parametric Mann-Whitney-Wilcoxon tests were used to compare means between unflooded and flooded sites for the following dependent variables: abundance of total taxa, species richness of total taxa, abundance of arboreal taxa, species richness of arboreal taxa, abundance of semi-arboreal taxa, species richness of semi-arboreal taxa, and abundance of 'refugees.' Mann-Whitney-Wilcoxon tests also were used to quantify relationships between flood status and proportional abundance of the following common, semi-arboreal taxa: *Argoctenus 'samueli'* sp. nov. (Araneae: Zoridae), *Supunna picta* (Araneae: Corinnidae), *Artoria hewquaensis* Framenau (Araneae: Lycosidae), *Battalus 'diadens'* sp. nov. Raven (manuscript name) (Araneae: Corinnidae), three ground-nesting *Camponotus* spp. (Hymenoptera: Formicidae) and *Iridomyrmex* sp. (*mattiroloi* group) (Hymenoptera: Formicidae).

Results

Forest-floor spiders

Eighty morphospecies of spiders (1125 individuals) were caught in pitfall traps over the three January 2001–2003 surveys (Chapter 4, Appendix 4.2). Ten species (533 individuals) were classed as semi-arboreal because they were caught on tree trunks both when the forest floor was flooded and dry. Sixty-four species (560 individuals) were classed as strictly terrestrial and six ground-active species (32 individuals) were classed as refugees because they were caught on trees only during floods (Chapter 4, Appendix 4.2). Two of the four most commonly pitfall-trapped spiders were semi-arboreal (Table 6.1).

No statistically significant relationships were found between flood patterns and the abundance and species richness of the total spider fauna or any of its components in January 2001 (Table 6.2a, Fig. 6.2) (see also Chapter Four). Change in these variables between January 2002–2003 also was not related to whether the site flooded in spring 2002.

Forest-floor ants

Forty-two morphospecies of ants (28 249 individuals) were pitfall trapped during the three January surveys (Chapter Five, Appendix 5.1). A single *Iridomyrmex* species (*mattiroloi* group) comprised 68.2% of pitfall-trapped ants. Twenty species (26 958 individuals) trapped on the forest floor also were trapped on tree trunks, although nine of those species (57 individuals) were classed as arboreal because they are known to nest in trees (Chapter Five, Appendix 5.1). A further two of those 20 species (4052 individuals) were abundant on the ground, but rarely were trapped on tree trunks.

The four most common species in pitfall traps all were ground nesters. Two of those species foraged extensively on tree-trunks even during flooding, while the other two

species were caught very rarely on tree trunks, suggesting the former used trunks as refugia and the latter do not (Table 6.3).

The mean change in species richness of ants between January 2002 and January 2003 differed between sites that flooded during that year and sites that had not flooded since spring/summer 2000-2001, indicating that the second flood was likely to have been associated with a decline in species richness of ants (mean \pm SD_{flooded spring 2002} = -2.00 \pm 1.41 (n = 4); mean \pm SD_{not flooded spring 2002} = 0.77 \pm 1.79 (n = 13), t = 3.21, df = 6.3, $P \approx$ 0.017). None of the other variables measured differed between sites that flooded and did not flood in spring 2002, except for the abundance of Rhytidoponera metallica (see below) (Fig. 6.3).

In January 2001, the total abundance and species richness of ants was lower on the forestfloor in areas that experienced extended flooding compared to sites that experienced moderate or brief/no flooding (Table 6.2b, Fig. 6.3) (see Chapter Five for further details). Both abundance and species richness of strictly ground-foraging ants was low in areas subject to extended inundation (Table 6.2b). Fewer trunk-foraging, ground-nesting ants were trapped on the forest floor in areas subject to protracted inundation; however, the species richness of that group did not differ between areas subject to different flood regimes (Table 6.2b). Ant species that forage on tree-trunks, as well as on the forest-floor, generally were ground-nesters. Thus, the capacity of the colony to shelter workers and reproductive individuals during flooding was considered to be of importance to the colony's ability to persist in regularly flooded areas. I observed ants sheltering under bark in flooded areas and noted that many more small ants than large ants can shelter under bark sheets of comparable size. Therefore, common ground-nesting, trunk-foraging ants were divided into large and small species.

The results presented here are for three Camponotus species combined (the most common large, ground-nesting trunk-foragers) and Iridomyrmex species (mattiroloi gp.) (the most common small, ground-nesting trunk-forager). Abundance of Iridomyrmex species (mattiroloi gp.) did not vary with duration of flooding in January 2001, but the larger

Camponotus spp. were more abundant on the forest floor at sites subject to shorter flooding or no flooding (Table 6.2b). Rhytidoponera metallica, a species identified as usually not active on tree-trunks, was less abundant on recently flooded sites compared with sites that did not flood during January 2001, but had densities similar to those on unflooded sites within one year (Table 6.2b). This result is consistent with the response of R. metallica to the 2002 flood. R. metallica abundance declined on the forest floor between January 2002 and January 2003 at sites that flooded in spring 2002 but not at sites that did not flood during that period (mean \pm SD flooded spring 2002 = -30.25 \pm 6.65 (n = 4); mean \pm SD not flooded $spring_{2002} = -9.54 \pm 32.52 \ (n = 13), t = 2.16, df = 14.4, P \approx 0.049).$

Tree-trunk spiders

Eighty-two morphospecies of spiders (1469 mature individuals) were caught on tree trunks. Sixty-six morphospecies (1077 individuals) were classed as exclusively arboreal. The fauna was numerically dominated by one species of arboreal, bark-dwelling clubionid (644 individuals) which comprised 43.8% of total spider catch. Ten species (368 individuals) were semi-arboreal (Chapter Four, Appendix 4.2). The most frequently trapped semiarboreal spiders were Argoctenus 'samueli' sp. nov.(Zoridae) (91 individuals), Artoria howquaensis (Lycosidae) (90 individuals) and Supunna picta (Corinnidae) (63 individuals). Battalus 'diadens' sp. nov. (Corinnidae: Castianierinae), an ant-mimic, often was trapped on tree trunks (74 individuals) and also on the ground at three sites. That spider closely resembled the ground-nesting, trunk-active ant Camponotus (nr. consobrinus). Abundance of the ant-mimicking spider was found to be highly correlated with abundance of Camponotus (nr. consobrinus) (Pearson r = 0.878, $P \approx 0.001$). That species was excluded from further analysis of semi-arboreal spiders because its distribution was not independent of ground-nesting Camponotus, which exhibited a complex flood-response. Only six species of spiders (24 individuals) normally restricted to the forest-floor were found on tree-trunks during floods.

The structure of the spider assemblages differed significantly between unflooded sites and currently flooded/recently emersed sites (ANOSIM R = 0.233, $P \approx 0.001$). The difference in spider assemblages between unflooded and flooded areas largely was attributable to variation in the abundance of semi-arboreal spiders (Table 6.4). However, the low values for the mean dissimilarity/standard deviation ratios indicated that the distribution of those species was highly variable and their influence was derived from sheer abundance, rather than from a consistent response to flooding (Table 6.4). No evidence was found for flood-related change in abundance or species richness of total spiders, exclusively arboreal spiders, semi-arboreal spiders or ground-dwelling spiders that only move onto trees during floods (only abundance tested) (Fig. 6.4).

Analyses of the individual flood responses of the most common species of semi-arboreal spiders revealed patterns that were obscured when spiders were grouped by habitat-use. *Argoctenus 'samueli'* sp. nov. (Zoridae) comprised a greater proportion of the trunk spider fauna at unflooded sites compared with flooded sites in November ($n = 5, 3 U = 15.0, P \approx 0.043$) and December ($n = 4, 4, U = 16.0 P \approx 0.018$) (Fig. 6.4). In November, *Battalus 'diadens'* sp. nov. (Corinnidae) comprised a greater proportion of spiders at dry sites ($n = 4, 4 U = 14.0, P \approx 0.045$); conversely *Supunna picta* (Corinnidae) made-up a larger proportion of the fauna at flooded sites ($n = 4, 4, U = 1.0, P \approx 0.043$) (Fig. 6.4). In October, *Artoria howquaensis* (Lycosidae) also comprised more of the trunk fauna at flooded sites than unflooded sites ($n = 3, 5, U = 0.00, P \approx 0.010$) (Fig. 6.4).

Tree-trunk ants

For ground-nesting ant colonies to survive flooding, ant reproductives (queens, fertilized workers) must seek refuge. It is difficult to assess movement of reproductives, so continual activity of workers on trunks of trees standing in floodwaters was taken as a surrogate for the colony seeking refuge.

Twenty-six species of ants (8022 individuals) were caught on tree trunks. Twelve species (1801 individuals) were classed as largely arboreal, including six species of *Podomyrma* (Andersen 1991) (Chapter 5, Appendix 5.1). Fourteen species (6193 individuals) were classed as trunk-active ground nesters. Two of those species (*Rhytidoponera metallica*, *Paratrechina sp. (obscura group)*), found to be highly abundant on the ground, were trapped very rarely on tree-trunks (28 individuals), suggesting that they do not forage extensively on tree trunks. No species was found to use tree trunks only during floods.

As with spiders, the composition of ant assemblages differed between unflooded and flooded/recently emersed sites (ANOSIM R = 0.254, $P \approx 0.001$). Variations in abundance of ground-nesting, trunk-foraging *Camponotus* and *Iridomyrmex* species between unflooded and flooded areas largely were responsible for these assemblage differences (Table 6.5). *Camponotus aeneopilosus* Mayr was one order of magnitude more abundant on tree trunks at unflooded sites compared to flooded/recently emersed sites. *C. aeneopilosus* had a relatively consistent distributional pattern with respect to flooding. The ratio of dissimilarity to standard deviation was 1.46 for *C. aeneopilosus*— the highest for any species (Table 6.5). A dissimilarity to standard deviation ratio ≥ 1.4 indicates that a species discriminates well between two habitats (Clarke and Warwick 1994).

Ground-nesting, trunk-foraging ants were more abundant on trees at unflooded sites during November ($n = 4, 4, U = 15.0, P \approx 0.043$) (Fig. 6.5). No response to flooding was evident in the total ant abundance, the abundance of fully arboreal ants, or the species richness of any group. Similarly, the proportion of ground-nesting *Camponotus* spp. and *Iridomyrmex* sp. (*mattiroloi* gp.) were not found to differ among flood treatments (Fig. 6.5).

Discussion

The forest floor and the trunks of river red gums each supported different spider and ant assemblages. Many species trapped on the forest floor were never caught on tree trunks. Similarly, tree trunks supported many specialized cortical taxa, such as two-tailed spiders (Hersiliidae). Therefore, not surprisingly, the two strata are experienced as different habitats by many invertebrates. However, different trapping methods were used to sample invertebrates on the forest floor and on tree trunks. The composition of samples would have been influenced by the trapping methods used. The biases inherant in pitfall trapping, used to sample the forest-floor fauna, are discussed in Chapter Three. Little is known about bias in arboreal photo-eclectors, used to sample the tree-trunk fauna. However, ants appear particularly adept at avoiding capture because workers that successfullysurmount the capturing area of the photo-eclector leave trace secretions to guide other ants along their path (Adis1981). Both trapping methods measure activity levels, rather than abundance were inferred from decreased activity. If flooding alters activity patterns, rather than abundance, the results may be misleading.

Some species were trapped on both the forest floor and tree trunks during floods and dry phases. There was some evidence to suggest that that using multiple habitats confers an advantage on species living in a highly variable environment. Semi-arboreal spiders comprised almost half of the total spiders trapped on the forest floor. The semi-arboreal habit of the widespread species *Argoctenus 'samueli'* sp. nov. probably explains why it was the only zorid spider found in high numbers in the floodplain forest (R. Raven, Queensland Museum, pers. comm.). Similarly, *Supunna picta* (Corinnidae)—a cosmopolitan generalist (*sensu* Jackson and Poulsen 1990; Goldsbrough *et al.* 2003), increased in proportional abundance on tree trunks when areas flooded. Furthermore, species of ground-nesting ants that use arboreal refugia persisted in areas subject to extended flooding, even though flooding was associated with a reduction in the total species richness of ants (Chapter Five).

There was no evidence of mass movement of spiders or ants into the canopy at the onset of flooding, despite compositional changes in tree-trunk assemblages at flooded sites. Few species so ght refugia outside their usual microhabitat during flooding; six species of spiders and no species of ant were found on tree-trunks only during floods. This result was unexpected, given that even relatively unpredictable flooding on European rivers causes a variety of normally ground-active taxa to climb trees (Adis and Junk 2002), and might be a product of the 'biotic resistance' of the cortical fauna. Similarly, Stone and Bacon (1994) did not find any evidence of an influx of invertebrate herbivores into the river red gum canopy following a flood-induced growth flush.

For some taxa, persisting in refugia for an extended period of time appeared to incur a cost. Flooding led to a proportional decrease in the abundance of the semi-arboreal spiders *Argoctenus 'samueli'* sp. nov. and *Battalus 'diadens'* sp. nov on tree trunks, although the decline in *B. 'diadens'* sp. nov. on tree trunks clearly was linked to lower activity of *Camponotus* prey in flooded areas. The activity of ground-nesting ants in trunk refugia at sites experiencing prolonged inundation remained relatively constant over spring, whereas activity at unflooded sites increased. Similarly, the abundance of ants known to use arboreal refugia was lower on the forest floor at sites recently subject to extended inundation, compared to sites that flooded for a shorter time. Negative effects of prolonged confinement in refugia probably arise from the restriction of foraging opportunities and intensification of biotic interactions because 'escape routes' are limited.

In contrast, the semi-arboreal spider Artoria howquaensis (Lycosidae) increased in proportional abundance on tree trunks when areas flooded. The hydrophilic wolf spider A. howquaensis was observed to hunt on Azolla filiculiodes Lam. mats floating on floodwaters. Because this spider could move between trees standing in floodwaters, it may not experience tree trunks as isolated refugia, hence A. howquaensis abundance was greater on tree trunks at flooded sites. This species is thought to use vegetation as a refugium from competition with larger ground-active lycosid spiders, rather than to escape drowning (sensu Gotch 2000). In the current study, Artoria howquaensis was only captured on forest-floor sites after a prolonged inundation period (Chapter Four).

The cost of prolonged arboreal refugia use experienced by semi-arboreal species did not translate into a benefit for the strictly arboreal fauna. Reduced competition from groundnesting species was expected to favour strictly arboreal species in flood-disturbed areas. Majer and Delabie (1994) found a higher proportion of the ant fauna in Amazonian floodplain forest was arboreal compared with upland forest, and this corresponded with a decline in ground-nesting species. Greenslade (1985) suggested that competition from ground-nesting species limits arboreal-nesting species in the sclerophyll forests of the Northern Territory, Australia. Similarly, Andersen and Yen (1992) found canopy-ant fauna to be dominated by ground-nesting species in the mallee region, and they described this result as typical for southern Australia. In the present study, trunk-foraging ant assemblages were numerically dominated by ground-nesting taxa. Ground-nesting ant activity was less on tree trunks in flooded areas, compared to dry areas, at the height of the inundation period (November). However, the present study provided no evidence that flood disturbance of the forest-floor ant assemblages confers any advantage on arboreal ants, as the abundance and species richness of strictly arboreal ants did not differ in relation to flooding.

Frequent flooding was not associated with a decline in the abundance or species richness of either the total forest-floor spider fauna or the strictly ground-dwelling component of the fauna. This suggests that other flood survival strategies are used successfully by groundactive spiders in river red gum forest. Floodwaters rise slowly in river red gum forest, potentially giving mobile species time to move to high ground away from the water.

Even when species are not successful at surviving floods, rapid re-colonization rates may enable them to exploit the floodplain habitat. For instance, the highly opportunistic species Rhytidoponera metallica persisted on the floodplain, despite not appearing to utilize arboreal refugia effectively. R. metallica activity was very low on sites immediately following flooding in 2000–2001. By summer 2002, when no flooding occurred, densities on sites flooded in 2000-2001 already had recovered to levels approximating sites that did not flood. In 2003, numbers again plummeted on sites that experienced a second flood (Fig. 6.3). In most species of Rhytidoponera, reproductively functional workers have taken the place of winged queens, making aerial dispersal of female nest founders impossible. R.

metallica is the only species from this genus known to retain occasional queen production (Ward 1986). No other species of Rhytidoponera was captured in this study. Plasticity of life-history traits may account for the ability of R. metallica to quickly re-colonize areas following flooding.

subtle ways.

Overall, flood response was highly taxon specific, a finding consistent with studies of aquatic invertebrates (e.g Thomson 2002). Lenihan et al. (2001) contended that few studies have investigated how disturbance effects propagate from the immediately perturbed area. The current study showed that the effects of flood disturbance propagate only weakly into the arboreal stratum, changing the composition of species assemblages on tree trunks in

In conclusion, use of multiple habitats confers an advantage to species in the perturbationprone floodplain environment because when one habitat type becomes untenable other habitats provide refugia. However, flooding does not suspend the factors that constrain species to particular habitats during the dry phase. Thus, unlike Amazonian floodplain forests where flooding creates habitat dynamism in three spatial dimensions, movement of habitat types appears to be restricted largely to the forest floor in river red gum floodplain forest, with the caveat that this study only investigated behaviour of flightless invertebrates on the lower trunks.

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Table 6.1. Habitats used by the most commonly pitfall-trapped spiders in river red gum floodplain forest.

Species	Percentage of total catch	Habitat use group
Argoctenus 'samueli' sp. nov.Raven	26.9%	Semi-arboreal
(Zoridae) (manuscript name)		
Artoria 'victoriensis' sp. nov.	6.3%	Strictly terrestrial?
Framenau, Gotch & Austin		
(Lycosidae) (manuscript name)		
Trochosa expolita (Simon)(Lycosidae)	5.9%	Semi-arboreal
Habronestes raveni Baehr (Zodariidae)	5.7%	Strictly terrestrial

Table 6.2. One-factor (duration of inundation) Analysis of variance results on January 2001 data for (a) spiders; (b) ants (Abundance data are square-root transformed).

DependentMean ± SEvariablebrief/nofloodingTotal spider3.55 ± 0.42abundanceErrorAbundance of3.14 ± 0.25strictly ground-active spidersError

(a)

Abundance of 1.20 ± 0.58 semi-arborealspidersError

Abundance of 0.85 ± 0.36 Argoctenus 'samueli' sp. nov. (Zoridae) Error

Abundance of 0.14 ± 0.38 Artoria howquaensis (Lycosidae) Error

Mean ± SE	Mean ± SE	Mean- square	F-ratio	 P
moderate	extended			
flooding	flooding			
3.34 ± 0.39	4.29 ± 0.37	2.138	1.749	0.198
		1.223		
2.69 ± 0.23	2.67 ± 0.22	0.541	1.235	0.311
		0.438		
1.77 ± 0.54	2.69±0.51	4.590	1.936	0.169
		2.371		
1.13±0.33	0.58 ± 0.31	0.631	0.709	0.503
	_		-	
		0.889		
0	0.88 ± 0.33	1.899	1.910	0.173
		0.995		

Table 6.2.	(a) continued
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Dependent	Mean \pm SE	Mean ± SE	Mean ± SE	Mean- square	F-ratio	P
variable	brief/no	moderate	extended			
	flooding	flooding	flooding			
Total spider species richness	6.29 ± 0.66	6.25 ± 0.62	6.11 ± 0.58	0.070	0.023	0.977
Error				3.039		
Specics richness of strictly ground-active spiders Error	4.71 ± 0.50	4.25 ± 0.47	3.78 ± 0.44	1.737	1.000	0.385
Species richness of semi-arboreal spiders Error	1.00 ± 0.41	1.75 ± 0.39	1.78 ± 0.36	1.451	1.216	0.316

Table 6.2. continued

(b)

Dependent	Mean \pm SE
variable	brief/no
	flooding
Total ant	21.55 ± 2.29
abundance (df =	
2)	
Error (df = 21)	
Abundance of	5.63 ± 0.66
strictly ground-	
active ants (df =	
2)	
Error (df ≈ 21)	
Abundance of	20.64 ± 2.30
trunk-foraging,	
ground-nesting	
ants	
Error	
Abundance of	6.58 ± 0.66
Camponotus spp.	
Error	
Abundance of	5.85 ± 0.75
Rhytidoponera	
metallica	
Error	

Mean \pm SE	Mean ± SE	Mean- square	F-ratio	P
moderate	extended			
flooding	flooding			
23.09 ± 2.14	13.94 ± 2.02	204.506	5.588	0.011
		36.597		
3.73 ± 0.62	0.81 ± 0.59	47.516	15.377	<0.001
		2 600		
		5.090		
2275+215	13 87 + 2 03	183 837	4 971	0.017
22.10 - 2.10	15.07 2 2.05	105.057	4.971	0.017
		36.983		
3.43 ± 0.62	2.23 ± 0.58	38.604	12.629	<0.001
		3.057		
2.87 ± 0.70	1.08 ± 0.66	45.145	11.447	<0.001
		3.944		

Table 6.2. (b) continued

Dependent	Mean ± SE	Mean ± SE	Mean ± SE	Mean- square	F-ratio	Р
variable	brief/no	moderate	extended			
	flooding	flooding	flooding			
Abundance of	17.96 ± 2.51	21.18 ± 2.35	12.93 ± 2.21	147.322	3.342	0.055
Iridomyrmex sp.						
(mattiroloi gp)						
Error				44.086		
Species richness	3.14 ± 0.43	2.38 ± 0.41	0.89 ± 0.38	10.669	8.111	0.002
of strictly						
ground-active						
ants						
Error				1.315		
~ · · ·						
Species richness	4.71 ± 0.35	4.50 ± 0.36	4.00 ± 0.38	1.098	1.076	0.359
of trunk-						
foraging,						
ground-nesting						
ants						
Error		<u> </u>		1.020		

	Percentage catch	of	total	Habitat use group
gp)	68.2%			Ground-nesting, extensive
				trunk-foraging
)	7.8%			Ground nesting, very limited
				trunk-foraging
llica	6.5%			Ground nesting, very limited
				trunk-foraging
layr	6.1%			Ground-nesting, extensive
				trunk-foraging

Table 6.3. Habitats used by the most commonly pitfall-trapped ants in river red gum

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Table 6.4. Species contributing most to dissimilarity in trunk-foraging spider assemblages between flooded and unflooded sites.

	Average abundance ± SE			
Species	Currently or recently flooded	Unflooded	Dissimilarity/ Standard Dev.	% Contributed to dissimilarity
Artoria howquaensis Framenau		··		
(Lycosidae)	5.8±2.4	2.0±0.7	1.12	7.7
(semi-arboreal)				
Battalus 'diadens' sp. nov. Raven				
(Corinnidae) (manuscript name)	0.3±0.1	5.5±2.1	1.03	7.3
(semi-arboreal)				
Argoctenus 'samueli' sp. nov. Raven				
(Zoridae) (manuscript name)	1.5±0.8	5.8±2.0	1.23	7.0
(semi-arboreal)				
Supunna picta (Koch) (Corinnidae)		1 510 5	1.15	6.0
(semi-arboreal)	3.9±1.2	1.5±0.5	1.15	3.9

Species

Camponot

(ground-ne

Iridomyrm

(ground-ne

Crematogo (arboreal

Camponot

'(ground-ne

Table 6.5. Species contributing most to dissimilarity in trunk-foraging ant assemblages between flooded and unflooded sites.

	Average abundance ± SE					
	Currently or recently flooded	Unflooded	Dissimilarity/ Standard Dev.	% Contributed to dissimilarity		
<i>us aeneopilosus</i> Mayr esting, trunk-foraging)	16.0 ± 3.5	165.2 ±75.9	1.46	16 3		
ex sp. (<i>mattiroloi</i> gp) esting, trunk-foraging)	4'2.4±11.5	102.6±57.5	0.96	10.8		
aster sp. (?))	51.6±24.9	37.9±7.1	1.26	9.1		
<i>tus</i> sp. (nr. <i>consobrinus</i>) esting, trunk-foraging)	5.2±3.4	34.3±15.0	1.30	9.0		

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Figure 6.1. Diagram of skirt-trap design.









2003.

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Figure 6.3. Changes in mean (\pm SE) abundance and mean (\pm SE) species richness of ants with different habitat-use characteristics on the forest floor January 2001-



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December (2002-2003).

345

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October November December

Month surveyed

Figure 6.5. continued

CHAPTER SEVEN

CONSERVATION MANAGEMENT

0.3 -

0.2 -

0.1

0.0

SYNTHESIS: THE CONTRIBUTION OF RIVER RED GUM FLOODPLAIN FORESTS TO INVERTEBRATE **BIODIVERSITY AND IMPLICATIONS FOR**

Knowledge gaps addressed by the current study

Ecologists increasingly are advocating the central tenet of the Flood Pulse Concept (FPC) model that a river and its floodplain are components of a single, integrated system (Junk *et al.* 1989). Testing of the FPC model has been restricted largely to aquatic taxa (but see Molles *et al.* 1998). This belies the dynamic nature of floodplain habitat, which alternates between an aquatic and a terrestrial phase. Despite their contribution to biodiversity and ecosystem processes, comparatively little research attention has focused on the response of terrestrial floodplain invertebrates to inundation (Ellis *et al.* 2001; Bonn *et al.* 2002). The system where non-aquatic invertebrates have received the most sustained research attention is the tropical Amazonian floodplain forest, which may function very differently to temperate river-floodplain systems (Adis and Junk 2002).

Studies of terrestrial floodplain invertebrates in temperate river-floodplain systems generally have considered only hydrophilic taxa, particularly ground beetles (Coleoptera: Carabidae) (e.g. Šustek 1994; Zulka 1994; Boscaini *et al.* 2000), rove beetles (Coleoptera: Staphylinidae) (e.g. Kunze and Kache 1998) and wolf spiders (Araneae: Lycosidae) (e.g. Wenninger and Fagan 2000). Hydrophilic terrestrial taxa probably have an important ecological role in transferring energy and nutrients across the aquatic-terrestrial interface (*sensu* Hering 1998). Establishing the connection between water flow regime and suitability of riparian habitat for hydrophilic species has relevance to conservation in regulated river-floodplain systems. However, in areas of floodplain that are not inundated many times per year, hydrophilic taxa may be a transient element of the fauna. The response of hydrophiles to flooding may not be representative of the response of other floodplain invertebrates. Therefore, understanding the ecology of floodplain invertebrates is contingent upon integrating the flood response of hydrophiles with that of species that are not considered to derive immediate benefit from flooding.

The FPC is limited to describing processes associated with flooding. It does not inform our understanding of ecological processes occurring on floodplains during intervals between

floods, beyond treating large floods as 'resetting' events (*sensu* Tockner *et al.* 2000). The current study sought to address these knowledge gaps in the context of temperate Australian floodplain forests. I tracked floodplain invertebrate assemblages for 32 mo in river red gum *Eucalyptus camaldulensis* floodplain forest to examine the response of both wet-phase and dry-phase taxa to flooding in the short- and long-term. How well the FPC models ecological processes shaping floodplain invertebrate assemblages was assessed both for hydrophilic taxa and for assemblages overall. The FPC postulates that "the flood-pulse is the major force controlling biota in river-floodplains" (Junk *et al.* 1989). Only by examining the relative importance of other factors influencing biota can this statement be appraised. Here, the effects of fallen timber on invertebrates were examined and compared with the effects of flooding. The findings of the study then are used to inform management recommendations for flooding and fallen timber in river red gum forest.

Response of wet-phase (hydrophilic and aquatic) taxa to flooding

In the short-term, flooding caused an influx of hydrophilic taxa to inundated areas of forest (Chapter Four). Ground beetles and wolf spiders were the most obvious components of this fauna. Flooding created a pulse in primary productivity and, consequently, an irruption of aquatic invertebrate populations. The presence of aquatic invertebrates appeared to attract predatory hydrophiles, increasing beetle biomass in extensively flooded areas by two orders of magnitude relative to unflooded sites (Chapter Four). In turn, the greater invertebrate biomass probably sustained higher insectivorous mammal populations (Chapter Four; Mac Nally and Horrocks 2002). Thus, the pulse in productivity created by flooding appears to be transfered among multiple trophic levels and across the boundary between land and water (cf. Polis and Hurd 1996) (Chapter Four).

Soon (4 mo) after floodwaters receded, hydrophiles largely disappeared from forest-floor habitat, although some wolf spiders were present for longer. The peaks in local hydrophile populations during inundation conformed to the FPC model of floodplains as pulse systems

(Junk et al. 1989; Tockner et al. 2000). Similarly, the transition between aquatic and terrestrial fauna in fallen timber was rapid. Four weeks after floodwaters receded, the assemblage of terrestrial invertebrates in recently submerged logs was very similar to the assemblage in logs that had not been inundated for 1-2 yr. The speed of the flood response indicates that colonists were likely to be present continually in refugia within the river red gum forest. Many of the hydrophilic species were considered to have generalized habitat requirements, beyond their need for moist conditions (Chapter Four)-a finding consistent with the characteristics of floodplain hydrophiles in temperate systems elsewhere (e.g. Adis and Junk 2002). Given their broad habitat requirements, these species were found on the margins of river channels and other damp microhabitats within river red gum forest.

Species that utilize channel edges are expected to be tolerant of limited changes in flood regime associated with river regulation (Chapter Four). However, in the present study, a preference of some terrestrial hydrophilic species for temporary wetlands was demonstrated (Chapter Four), suggesting that at least part of the fauna is likely to be affected adversely by flood mitigation. A general lack of knowledge of the habitat requirements of Australian invertebrates makes it difficult to assess the habitat range of species and, hence, their vulnerability to habitat change. For instance, Anomalosa kochi (Simon) (Lycosidae) was captured regularly, but previously was known only from tropical Queensland (Lehtinen and Hippa 1979; V.W. Framenau, Western Australian Museum, pers. comm.).

The provision of humid microhabitats by flooding partially accounts for the occurrence of some species in river red gum forest that, although not considered hydrophilic, are typically associated with humid rainforests rather than dry sclerophyll forest. 'Gondwanan relicts' present in river red gum forest included representatives of the spider families Cyatholipidae and Pararchaeidae (York Main 2001; cf. Eskov 1987), as well as a beetle species from the family Byrrhidae (Matthews1985). Matilda sp. (Cyatholipidae) is sclerotized to reduce water loss, consistent with this genus being found in sub-humid river red gum forest when other cyatholipid spiders are restricted to rainforests (Raven et al. 2002). In contrast, Pararchaea nr. binnaburra (Pararchaeidae) showed no obvious morphological adaptations to xeric conditions. Indeed, the morphology of this ancient lineage of spiders is conservative, which was thought to restrain the Pararchaeidae entirely to rainfcrest (Forster and Platnick 1984). The inability of the Pararchaeidae to tolerate xeric conditions suggests that Pararchaea nr. binnaburra was dependent on moist microhabitats within the generally sub-humid river red gum forest.

Responses of dry-phase taxa to flooding

For non-hydrophilic taxa, the flood pulse was thought to cause 'catastrophic' population declines in the short-term (Adis and Junk 2002). However, the role of the flood-pulse in shaping floodplain biodiversity over the longer term largely has been ignored (but see Molles et al. 1998). In the current study, when the variability in abundance and species richness of beetles, spiders and ants were considered over 32 mo, it was evident that flooding did not produce large, discrete troughs (or peaks) in non-hydrophilic invertebrate populations. For instance, immediately after the recession of floodwaters, ant activity was least at sites that were inundated for the longest time. However, when compared to interannual and inter-seasonal variation, the decline in ant activity was moderate (Fig. 5.1).

Flooding was associated with persistent, long-term differences in invertebrate assemblages, rather than short-term differences. Two years after the major flood, the assemblage structures of beetles, spiders and ants differed between sites that experienced extended inundation and brief or no inundation (Chapters Four and Five). Moreover, many of these differences were apparent before the 2000-2001 flood occurred. The response of invertebrates to flooding was taxon specific. Flooding was associated with sustained greater species richness of beetles, reduced species richness of ants and little change in the species richness of spiders.

Differences in the structure of the river red gum canopy between flood-prone and drier areas is the most likely explanation for the persistent differences in the fauna. In floodprone areas, river red gums are taller due to the availability of floodwaters sustaining longer growing periods (Boomsma 1950; Dexter 1978). Flooding causes a flush of foliage growth
(Stone and Bacon 1995), associated with the creation of a deeper litter layer. Therefore, not only do flood-prone areas received more water through flooding but the capacity to retain moisture is enhanced by greater shading and the 'mulch' provided by leaf litter and fallen timber. Despite the species composition of the canopy being identical, ground-active invertebrates experienced flood-prone and drier areas of river red gum forest as different habitats. In this respect, flooding is the major factor shaping invertebrate assemblages. Therefore, the FPC model is applicable to non-hydrophilic floodplain invertebrates, but there is a need to explicitly consider the lasting impact of the flood pulse on habitat structure.

Despite flooding being associated with a decrease in the abundance and species richness of ants, the ground-active invertebrate fauna numerically was dominated by ants. The mean $(\pm SE)$ summer catch of ants in the pitfall traps across all sites was 392 ± 38 , compared to 18 ± 2 beetles and 16 ± 1 spiders. While the limitations of pitfall trapping for assessing relative abundance are recognized, such a large disparity in catch size suggests that ants are the most 'successful' taxon at exploiting this floodplain habitat. Ants were able to use arboreal flood refugia (Chapter Six) and hence, recolonized areas soon after floodwaters receded (Chapter Two and Chapter Five).

Importance of other habitat factors—the role of fallen timber

Much emphasis has been placed on the role of hydraulic conditions in shaping the floodplain habitat. The effects of factors that structure habitat locally have not been well studied. Fallen timber has been identified as an important resource in forest-floor habitats generally (Harmon *et al.* 1986) and in riparian forests (Braccia and Batzer 2000). In the present study, the role of fallen timber as habitat and as a structural element of the forest floor was examined and its influence compared to that of flooding.

Obligate saproxylic species largely were absent from logs on the floodplain, with the exception of the termite *Coptotermes acinaciformis* (Froggatt) in less flood-prone areas. Despite the paucity of the specialist saproxylic fauna, logs provided a structurally complex substrate. Logs were utilized as nesting sites by ants during the dry phase and, when submerged, rapidly were colonized by aquatic invertebrates which grazed on the biofilm that formed on the logs (e.g. the chironomid *Kiefferulus* sp.) (Scholz and Boon 1993) (Chapter Two). The richness of the dry-phase fauna increased in more structurally intricate logs, but the composition of the invertebrate assemblages was determined by the flooding-history of logs. Thus, both large-scale flooding and small-scale habitat structure influence the biota. Logs also enhanced the complexity and heterogeneity of the forest floor habitat by trapping leaf litter. At small spatial scales, greater amcunts of leaf-litter near logs was linked to increased abundance and richness of invertebrates on the forest floor (Chapter Three). However, these relationships did not hold at the scale of 0.25 ha sites, suggesting that other factors, such as flooding, operating at the site scale obscure the influence of fallen timber.

Consequences of habita regimes

The forest-floor invertebrate fauna comprised four main elements: (1) aquatic taxa; (2) hydrophilic terrestrial species; (3) terrestrial opportunistic species with generalized lifehistory traits and; (4) species with arid-zone affinities. Any change to the flood regime is expected to alter the constitution of the invertebrate assemblages of the forest-floor (Fig. 7.1). Moreover, changed flooding regimes are expected to affect the arboreal fauna too (Chapter Six). Although responses to changes in flood regime are species-specific, it is possible to make some generalizations.

Consequences of habitat change for fauna-disruption to natural flood

First, the composition of the aquatic-invertebrate assemblages in floodplain wetlands is controlled by the frequency, duration and seasonality of inundation (Boulton and Brock 1999; Hillman and Quinn 2002). The probable impacts of changes in flood regimes on aquatic invertebrates in river red gum floodplain wetlands have been considered (see Boulton and Lloyd 1991; Boulton and Lloyd 1992; Quinn *et al.* 2000). Reduction in flooding should decrease the available habitat for hydrophilic terrestrial invertebrates, especially those species that depend on temporary, lentic-wetland habitats created by flooding. Disruption of flooding could, therefore, reduce hydrophile population sizes. Ellis *et al.* (2001) found that increases in populations of hydrophilic ground beetles were delayed until after a second managed flood in an arid-zone, floodplain-river system in the United States of America. It may be that the capacity of hydrophilic invertebrate populations to respond to the flood pulse is compromised when population sizes fall below a threshold level. In turn, this would be expected to affect ecological services performed by terrestrial hydrophiles, such as the transfer of energy and nutrients between aquatic and terrestrial habitats.

Species with opportunistic, generalized life-history characteristics, such as the corinnid spider *Supunna picta* (Koch), are expected largely to be insensitive to changes in flood regime. In the long-term, increases in biotic interactions associated with greater habitat stability may reduce populations of some species. In the current study, predation by anteating spiders, but not competition between ants, appeared to decrease following flood perturbation (Chapter Five). However, biotic interactions *per se* were not examined experimentally.

In contrast, the arid-adapted element of the fauna is expected to benefit from reduced flooding. The presence of xeric-adapted species on the floodplain reflects the position of the study area in an overlap zone between temperate and semi-arid regions. Arid-zone specialists included members of the same families as the hydrophilic taxa, such as the xeric-adapted carabid beetles *Geoscaptus laevissimus* Chaudoir and *Calosoma* (?)schayeri Erichson (Matthews 1980). Other arid-zone specialists included spiders from the families Gallieniellidae (e.g. Meedo cohuna Platnick) and Zodariidae (e.g. Pentasteron intermedium Baehr and Jocque) (Raven et al. 2002; Baehr and Churchill submitted), as well as ants from

the genus *Melophorus* (Shattuck 1999). Species considered to be arid-adapted were intolerant of flooding or flood-associated habitat change (e.g. Zodariidae; Fig. 5.6).

If flooding was suspended, the species richness of ground-active ant assemblages at previously flood-prone areas gradually should increase to match that of the drier areas. However, because of the 'lag' created by differences in habitat structure, the time horizon for such a convergence to occur is decades long. Hering (1995) found that reduction in flooding shifted the balance of competition to favour ants at the expense of beetles in a European river-floodplain system. The faunal assemblages in river red gum forest is unlikely to show a similar response. The numerical dominance and ubiquity of ants in the sub-humid floodplain forest suggests that habitat loss, rather than competition, is the proximate mechanism by which reduced flooding affects beetles.

Consequences of habitat change for fauna-removal of fallen timber

Individual logs have a demonstrable influence on the forest-floor fauna at the 5-m scale, but this effect is not evident at the 0.25 ha scale, making it difficult to elucidate the biodiversity implications of removing large volumes of fallen timber. Clearly, it is not appropriate to simply 'scale-up' the results based on measurement of individual logs, yet, equally, the small-scale results demonstrated that logs do promote invertebrate biodiversity, even if the effect is not clear at larger spatial scales. During floods, submerged logs were colonized by large numbers of aquatic invertebrates. Mean densities of the chironomid larva *Kiefferulus* sp. on logs reached 1190 \pm 374 m⁻² after a 6-wk immersion. Maher and Carpenter (1984) suggested that flood-induced chironomid abundance is important to waterfowl breeding. Similarly, an insectivorous bird, *Climacteris picumnus* Temminck, and an insectivorous marsupial, *Antechinus flavipes* (Waterhouse), increased in abundance in river red gum forest only when a threshold load of 40 t ha⁻¹ of fallen-timber was exceeded (Mac Nally and Horrocks 2002; Mac Nally *et al.* 2002). Therefore, removing fallen timber is expected to have negative impacts on some species.

Conclusions and conservation management

River red gum floodplain forests provide habitat for numerous ground-active invertebrates, including more than 242 species of beetles, 162 species of spiders and 47 species of ants (Appendices 4.1, 4.2 and 5.1). Flooding causes pulses in populations of aquatic and hydrophilic invertebrates, with ramifications through the entire food web. However, the most persistent and perhaps the most influential effect of flooding is the creation of a mosaic habitat structure, critical to sustaining invertebrate diversity. At least at small spatial scales, fallen timber influences invertebrate assemblages, but these scales are too small to inform management actions.

Managed environmental flows attempt to mimic natural flood regimes. The current study has demonstrated the importance of managed flooding for invertebrate assemblages. On the regulated rivers in the Murray-Darling Basin, environmental flows are the means to initiate pulses in populations of aquatic invertebrates and terrestrial hydrophiles. Moreover, environmental flows are necessary to maintain the habitat heterogeneity that here was demonstrated to promote invertebrate biodiversity, both by creating alternating wet-dry habitats and by causing local differences in the canopy structure. Duration of flooding was shown to be an important factor regulating invertebrate assemblages. Longer floods are known to benefit other taxa (e.g. breeding waterbirds, Barmah-Millewa Forum 2001). Therefore, environmental flows should be managed to mimic the duration, as well as the frequency, of natural flooding. The annual Environmental Water Allocation made to the Barmah Forest has a tangible biodiversity benefit and should be maintained.

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- Canopy sparse, open ٠
- Little leaf litter ٠
- Species richness of ants is relatively high
- Species richness of beetles is relatively ٠ low
- Abundance of ant-eating spiders is high

Areas with regular flooding during the dry phase

- Canopy fuller, less open •
- Leaf litter piles against logs forming a species-rich micro-habitat
- Species richness of ants is low, only floodtolerant species persist
- Species richness of beetles is greater than in areas without regular flooding ٠
- Ants nest in fallen timber • ´

Areas with regular flooding during the wet phase

- Canopy undergoing growth flush ٠
- Influx of hydrophilic spiders and beetles
- Biomass of beetles increases 100x .
- Species richness of beetles is greater than in areas without regular flooding ٠
- Flood-tolerant ants move into arboreal ٠ refugia
- Aquatic taxa colonize submerged fallen ٠ timber

Figure 7.1. Schematic of the response of ground-active invertebrates to different flood