Ecological niche breadth and microhabitat guild structure in temperate Australian reptiles: Implications for natural resource management in endangered grassy woodland ecosystems.

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Abstract Ecological theory predicts that species with narrow niche requirements (habitat specialists) are more vulnerable to anthropocentric disturbances than those with broad niche requirements (habitat generalists). Hence, understanding a species ecological niche and guild membership would serve as a valuable management tool for providing *a priori* assessments of a species extinction risk. It also would help to forecast a species capacity to respond to land use change, as what might be expected to occur under financial incentive schemes to improve threatened ecological vegetation communities. However, basic natural history information is lacking for many terrestrial species, particularly reptiles in temperate regions of the world. To overcome this limitation, we collated 3527 reptile observations from 52 species across an endangered woodland ecoregion in south-eastern Australia and examined ecological niche breadth and microhabitat guild structure. We found 30% of species had low ecological niche values and were classified as habitat specialists associated with large eucalypt trees, woody debris, surface rock or rocky outcrops. Cluster analysis separated species into six broad guilds based on microhabitat similarity. Approximately 80% of species belonged to guilds associated with old growth vegetation attributes or non-renewable litho-resources such as surface rock or rocky outcrops. Our results suggest that agri-environment schemes that focus purely on grazing management are unlikely to provide immediate benefits to broad suites of reptiles associated with old growth vegetation and litho-resources. Our classification scheme will be useful for identifying reptile species which are potentially vulnerable to anthropocentric disturbances and may require alternative strategies for improving habitat suitability and reptile conservation outcomes in grassy woodland ecosystems.

Keywords: Agri-environment scheme, box gum grassy woodland, community composition, reptile diversity, vegetation management.

INTRODUCTION

The application of theory in conservation biology provides a useful framework for understanding environmental complexity (Wiens 1995; Turner *et al.* 2001; McGlade 2009). However, Driscoll and Lindenmayer (2012) argue that many ecological theories are heuristic, poorly defined and narrowly focused, and fail to deliver adequate conservation outcomes. The 'niche' concept is one realm of theoretical ecology that has been the subject of much debate since its conception (Whittaker *et al.* 1973; Pianka 1976; Kearney 2006; Holt 2009; McInery & Etienne 2012). The original concept, coined by Joseph Grinnell, used the term ecological niche to describe the basic habitat a species requires to survive and reproduce (Grinnell 1917). Elton (1927) further contextualized the concept of niche in terms of the trophic role of a species in the community. However, it was not until Hutchinson (1957) made the distinction between the fundamental (ecological) niche and the realized (actual) niche of a species (i.e. after resource competition and predator-prey interactions had taken place) that the concept became widely applied (reviewed by Whittaker *et al.* 1973; Leibold 1995; Austin 2007; Peterson 2011). Despite the growing literature on the application of niche theory in ecology, for many organisms, their fundamental niche remains poorly known.

Space, time and food are all important dimensions of the ecological niche of an organism (Pianka 1973; Peterson 2011). However, when applied to management, habitat descriptors are more important than time and food in explaining niche partitioning (Schoener 1974). This is because the ecological niche provides insights into a species extinction risk and vulnerability to anthropocentric disturbances (Owens & Bennett 2000; Botts *et al.* 2013). Several studies have found that species most at risk of decline or extinction are habitat specialists (Foufopoulos & Ives 1999; Owens & Bennett 2000; Lee & Jetx 2011). Reptiles as a group are perceived to be more susceptible to threat processes than birds or mammals due to their relatively narrow range distributions and niche requirements (Gibbons *et al.* 2000). However, managing multiple species over large spatial scales is problematic (Fischer *et al.* 2004), and strategies to improve biodiversity outcomes in human-modified landscapes are required. The strategy of mesofilter conservation may provide some solutions to this problem of managing multiple species (Hunter 2005). This strategy seeks to manage ecosystems to benefit many species simultaneously. The effectiveness of mesofilter conservation is dependent on the ability to identify key elements of a landscape that are critical to broad suites of species (Mac Nally 2004). Guild-based investigations that identify critical habitat components for groups of organisms can provide a mechanism for managing multiple species (Holmes *et al.* 1979; Mac Nally 1994; Kornan *et al.* 2013). However, to the best of our collective knowledge, no studies have explicitly quantified niche breadth and guild structure in temperate Australian reptiles. Thus, understanding a species ecological niche and guild membership not only provides a useful management tool for predicting species responses to disturbance, but can also provide an *a priori* assessment of a species capacity to respond to environmental change.

To provide critical information to guide reptile conservation in the context of native vegetation management, we examined ecological niche breadth and guild membership in a temperate woodland reptile community from south-eastern Australia. This broad region supports the critically endangered white box-yellow box-Blakely's red gum woodland (referred to as box gum grassy woodland) and derived native grassland ecological vegetation communities. These ecological vegetation communities are two of the most heavily cleared and modified bioregions in the world (Benson 2008). Furthermore, the region is rich in reptile diversity (Kay *et al.* 2013) and contains several threatened species, including the nationally vulnerable pink-tailed worm lizard *Aprasia parapulchella* (Environment Protection and

Biodiversity Conservation Act 1999) and the endangered northern velvet gecko *Amalosia rombifer* (Threatened Species Conservation Act 1995). However, reptiles in the temperate woodlands of south-eastern Australia have been poorly studied, especially within the box gum grassy woodland, and little natural history information is available for the vast majority of species in the ecoregion.

In recent years, the Australian Government (Commonwealth of Australia 2009), Local Land Services in New South Wales and Catchment Management Authorities in Victoria have delivered market-based incentive schemes that pay private land managers (often farmers) to undertake specific conservation actions as part of funding agreements to improve box gum grassy woodland vegetation condition and extent (Lindenmayer *et al.* 2012). These instruments are referred to as agri-environment schemes. However, a key assumption of the agri-environment scheme is that changes in livestock grazing management and pest plant control will facilitate improvements in native vegetation condition. This will, in turn enhance habitat for woodland fauna. However, recent studies that have evaluated reptile responses to agri-environment schemes and native vegetation management in general report limited success in terms of improving reptile species richness and diversity (Brown *et al.* 2011; Dorrough *et al.* 2012, Michael *et al.* 2013, 2014). A broader understanding of the mechanisms that drive species response to landscape change is required to inform and improve future management incentive schemes. With the aim of improving conservation outcomes, we sought to identify species with narrow niche requirements (habitat specialists) and microhabitat guilds associated with landscape elements that are not adequately captured under conventional management schemes. We use this information to determine which species are likely to require a targeted management approach to improve habitat suitability and reptile conservation outcomes in farming landscapes.

METHODS

Study area

We conducted our study in the temperate eucalypt woodlands of south-eastern Australia, and predominantly within the critically endangered white box *Eucalyptus albens*, yellow box *E. melliodora* and Blakely's red gum *E. blakelyi* grassy woodland and derived native grassland ecological vegetation communities. Our study region extended from Warwick in southern Queensland (28°01S 152°11E) to Merton in southern Victoria (36°58' 145°42') and spanned a latitudinal distance of approximately 1,130 km (Fig. 1). The average annual rainfall in the region ranged from 696 mm in the north, peaking in the summer months (Warwick weather station No. 41525), to 710 mm in the south, peaking in the winter months (Alexandra weather station No. 88001). The average annual minimum and maximum summer temperatures ranged from 17.9°C - 30.0°C in the north to 11.9°C - 29.3°C in the south. The average annual minimum and maximum winter temperatures ranged from 2.9°C - 17.9°C in the north to 2.5°C - 11.2°C in the south (BOM 2013).

Temperate eucalypt woodlands once formed a relatively continuous band of vegetation on fertile soils west of the Great Dividing Range from approximately 27° S in southern Queensland to the lower south-east of South Australia (Yates & Hobbs 2000). Today, more than 95% of the temperate woodland has been cleared and converted to agriculture (Lindenmayer *et al.* 2010). In recognition of the growing concern about biodiversity conservation issues in production landscapes, the Australian Government developed the Environmental Stewardship Program. This program, which is congruent with the European Union's agri-environment scheme, aims to maintain and/or improve the condition and extent of threatened woodland ecological vegetation communities under the *Environment Protection and Biodiversity Conservation Act* 1999. Agri-environment schemes provide private land managers with the financial incentive to undertake prescriptive management interventions, including modifying grazing regimes, reducing fertilizer use, undertaking exotic plant management, restricting timber and rock removal and planting native understorey species.

Experimental design and survey protocol

We established 677 sites on private property across the region as part of five long-term biodiversity monitoring programs (see Table 1 for a description of each program). Each site consisted of a 200 m transect marked at the 0 m, 100 m and 200 m points. Grazing management varied at each site and included areas under set stocking, rotational grazing (e.g. spring – summer grazing exclusion) or total grazing exclusion. Between 2002 and 2012, we conducted 2,652 site visits across the five programs, representing between three and five survey periods (Table 1). We completed surveys between August and December and between 0900 and 1600 hours on clear, sunny days with minimal wind. At each site, one observer conducted a time- and area- constrained (30 min x 1 ha) active search of natural habitat (200 m x 50 m), whereby reptiles were captured by hand or visually identified *in situ*. For each observation, we recorded the microhabitat (substrate) where the reptile was first sighted, assigning the record to one of eight microhabitat types: open ground = OG (including among grass), leaf litter = LL (beneath or on top), on log = OL (including fallen trees), on rock = OR (boulder or outcrop), tree trunk = TT (including tree stumps and dead trees), under bark of large trees = UB, under log = UL, and under surface rock = UR.

Data analysis

For each species, we calculated Levin's measure of niche breadth using the inverse of Simpson's diversity index (Simpson 1949):

$$B = 1/\sum_{i=1}^{n} p_i^2$$

Where *B* is the microhabitat niche breath value, *i* is the microhabitat category, *n* is the number of categories, and *p* is the proportion of microhabitat category *i*. The form of the Simpson's diversity index varies from 1 which represents a single microhabitat category to *n*, representing equal use of a given number of categories. We classified species with $B < 1.5$ as habitat specialists and species with $B > 1.5$ as habitat generalists based on a natural break in the histogram of niche values. To explore guild membership, we created a similarity matrix in Primer v6 (Clarke & Gorley 2006) and performed a cluster analysis using the Bray-Curtis similarity index on the standardized frequency distributions for species microhabitat use. Twelve species (23%) were recorded less than twice and were omitted from the cluster analysis.

RESULTS

Summary statistics

Our data comprised 4287 observations from 52 species in ten families (Table 2). From the total number of observations, we obtained microhabitat data from 3527 individuals. The three most abundant species that accounted for over 65% of all observations were Boulenger's skink *Morethia boulengeri* (*n* = 1159, 32.8% of observations), ragged snake-eyed skink *Cryptoblepharus pannosus* (*n* = 959, 27.2% of observations) and the eastern striped skink *Ctenotus robustus* (*n* = 238, 6.7% of observations).

Niche breadth

Microhabitat niche breadth (*B*) ranged from 1.00 to 4.01 (Table 2). Mean niche breadth values were highest in the family Scincidae (*n* = 22 species, *B* = 2.09), followed by Agamidae (*n* = 5, *B* = 1.92), Pygopodidae (*n* = 5, *B* = 1.83), Elapidae (*n* = 8, *B* = 1.7), Gekkonidae (*n* = 9, *B* = 1.66) and Typhlopidae (*n* = 2, *B* = 1.13). Twenty-three species (44%) had niche values less than *B* = 1.5. After removing species with less than two observations, we classified 12 species (30%) as habitat specialists (Table 2). These included *Amphibolurus burnsi*, *A. muricatus*, *Hemiergis talbingoensis*, *Ramphotyphlops nigrescens*, *Tiliqua scincoides*, *Egernia cunninghami*, *Aprasia parapulchella*, *Ctenotus teaniolatus*, *Diplodactylus vittatus*, *Lerista bougainvillii*, *R. weidii* and *Underwoodisaurus milii* (Table 3).

Guild classification

Our cluster analysis grouped species according to habitat similarity (number of microhabitats used and frequency of use) and produced six broad guilds: 1) saxicolous (outcrop-dwelling); 2) arboreal; 3) semi-arboreal; 4) fossorial (log-dwelling); 5) cryptozoic (surface rock-dwelling) and 6) four terrestrial sub-groups (Table 3). Saxicolous members included two species from Scincidae; arboreal guild members included four species from Gekkonidae; semi-arboreal members included seven species from Agamidae, Scincidae and Varanidae; fossorial members included six species from Scincidae, Gekkonidae and Typhlopidae; cryptozoic members included ten species from Pygopodidae, Scincidae, Gekkonidae, Typhlopidae and Elapidae; and the four terrestrial sub-groups included ten species from Pygopodidae, Scincidae and Elapidae (Table 3). Frequency distributions for all 52 reptile species according to their microhabitat categories are provided in the supporting information (S1-7).

DISCUSSION

We evaluated ecological niche values and habitat guild structure in a reptile community associated with the endangered box gum grassy woodland in south-eastern Australia. Our key findings were: 1) 30% of the reptile community had low ecological niche breadth values and were classified as habitat specialists. These species were associated with logs, surface rocks, rocky outcrops or mature trees. 2) 80% of all species belonged to habitat guilds associated with old growth attributes or non-renewable litho-resources. We discuss the implications of our classification scheme in the context of vegetation management, market-based financial incentive programs and agri-environment schemes.

Niche breadth

Habitat specialists are predicted to be more vulnerable to disturbance than habitat generalists (Brown *et al.* 1995; Thuiller 2004; Botts *et al.* 2013). In this study, many species were infrequently observed and for these species, niche breadth values should be interpreted with caution. Among those species with sufficient data, we classified twelve species as microhabitat specialists (Table 3). Five of these species were associated with attributes of old growth vegetation, such as large mature eucalypt trees and fallen timber. The remaining seven species were associated with non-renewable resources such as surface rock (bush rock) and insular rocky outcrops (predominantly granite) (Table 3).

Species that are adapted to specific environments over their geographical range (i.e. species with a narrow ecological niche) may not be able to respond to changes in the landscape that result from human disturbances (Gehrig & Swihart 2002), including those that occur under traditional farming practices. Examples include incremental loss of large paddock trees (Fischer *et al.* 2009), loss of fallen timber (Mac Nally *et al.* 2001; Manning *et al*. 2013) and bush rock removal and outcrop degradation (Michael *et al.* 2010). Hence, species that rely on large trees, fallen timber or surface rocks are most vulnerable to local extinction due to the incremental loss of these critical habitats in agricultural landscapes. Once depleted, old growth resources such as fallen timber may take several decades to accumulate, and surface rock may never be replaced. A logical extension of this concept is that habitat specialists also may not respond immediately to improvements in native vegetation condition and extent, such as those reported to occur under agri-environment schemes (Lindenmayer *et al.* 2012; Michael *et al.* 2014) or land abandonment (Lunt *et al.* 2010). In one study, Michael *et al.* (2014) found that only habitat generalists such as *M. boulengeri* and *C. pannosus* responded to native vegetation management. Similarly, Dorrough *et al.* (2012) argue that most reptiles are unlikely to respond to the short-term benefits gained by rotational grazing management. Clearly, more work needs to be done to enhance conditions for habitat specialists.

Guild classification

Many ecological communities contain guilds (Pianka 1980), groups of organisms which strongly interact among themselves for the use of a common resource, but only weakly with members of other groups (Blaum *et al.* 2011; Peterson 2011). In the context of wildlife management, understanding how different communities are structured in terms of guild assemblages is important for determining which groups of species are reliant on resources that may be limited or depleted in the landscape. Our cluster analysis grouped 39 species based on microhabitat similarity (Fig. 2). From this we were able to distinguish six broad microhabitat guilds within the box gum grassy woodland (Table 3). Notably, 80% of all species belonged to guilds associated with old growth attributes (e.g. fallen timber and large old trees) or non-renewable resources (e.g. surface rocks and rocky outcrops).

The strong reliance on old growth trees and tree-related resources such as fallen timber by several guilds (arboreal, semi-arboreal and fossorial) raises an important issue in the conservation of reptiles in agricultural landscapes - the management of fallen timber and firewood collection. The collection of fallen timber for firewood or to simply clean up paddocks is a widespread and common practice in Australian grazing landscapes. This practice has significant negative outcomes for reptiles (Driscoll *et al.* 2000; Mac Nally *et al.* 2001; Manning *et al.* 2013, Michael *et al.* 2014). More strategic policies on timber management are required given that so many reptile species are dependent on fallen timber for thermoregulation, shelter and foraging (Mac Nally *et al.* 2001; Manning *et al.* 2013). Furthermore, more research is required to evaluate threshold responses to amounts of fallen timber to develop ecologically sustainable prescriptions for timber collection on private property. A recent study in the Australian Capital Territory examined reptile responses to timber restoration and found that reptile abundance increased significantly over a four year period in response to the addition of timber into a grassy woodland reserve (Manning *et al.* 2013). That study suggested some reptile species (e.g. terrestrial generalists) may respond relatively quickly to timber retention and the strategic re-introduction of timber to grazing landscapes.

A second major issue in the conservation of woodland reptiles is the management of bush rock and insular rocky outcrops. Our classification scheme identified a wide variety of cryptozoic and saxicolous species associated with this non-renewable resource (Table 3). The cryptozoic guild also includes the Nationally Endangered pink-tailed worm lizard *A. parapulchella*. This species has a patchy distribution throughout the southern half of the box gum grassy woodland and the importance of shallowly-embedded surface rocks in the ecology and conservation of this species is well established (reviewed by Wong *et al.* 2011). However, for the vast majority of other cryptozoic species, including *R. weidii* (a small scolecophidian snake which occupies the same niche as *A. parapulchella*), habitat requirements are poorly known and it is likely that their distribution is limited and strongly influenced by the presence of rocks in the landscape. From a management perspective, the collection of bush rock presents a major threat to temperate reptiles (Pike *et al.* 2010; Croak *et al.* 2013) but is an activity that is difficult to regulate (Shine *et al.* 1998). In the box gum grassy woodland, bush rock retention is primarily limited to short-term funding agreements under the Environmental Stewardship Program. Bush rock removal is listed as a threatening process under Schedule 3 of the New South Wales *Threatened Species Conservation Act* (1995). However, the listing exempts “the removal of rock from paddocks when it constitutes a necessary part of the carrying out of a routine agricultural activity” (see supporting information for an example of bush rock removed from a paddock).

Because ‘bush rock’ is non-renewable and several key reptile guilds are dependent on this resource (Table 3), it should be a key component of environmental stewardship payments and other agri-environment schemes to address reptile conservation in agricultural landscapes. Furthermore, Australian states need to adopt policies on busk rock removal in the wider agricultural landscape to prevent incremental loss of this keystone resource. Michael *et al.* (2008, 2010) provide a case for managing rocky outcrops in agricultural landscapes, emphasizing the importance of protecting this resource to maintain and enhance reptile diversity. Rocky outcrops also provide important nodal points in the landscape from where restoration efforts could be focused. Physical restoration of rocky outcrops should also be considered. For example, in the Sydney region, artificial rocks have been used successfully to restore degraded habitat for threatened reptiles (Webb & Shine 1999; Croak *et al.* 2010; Croak *et al.* 2013). This method could be applied to granite outcrops, especially those where exfoliated surface rock has been removed or damaged by livestock. However, a major deficiency in agri-environment schemes and natural resource management in general in south-eastern Australia is the lack of policy guidelines on protecting and managing rocky outcrops.

Implications for natural resource management

A relatively recent initiative of State and Federal governments in Australia is to provide land managers with financial assistance to "improve the condition and extent of endangered ecological communities such as box gum grassy woodland" by reducing stocking and grazing intensity, reducing fertiliser use, expanding weed management and replanting native species (Commonwealth of Australia 2009). Studies that evaluate the merits of native vegetation management interventions for improving faunal diversity are generally lacking in Australia (Lindenmayer *et al.* 2012). Two recent studies indicate that reptiles are unlikely to respond to short-term changes in grazing regimes (Dorrough *et al.* 2012; Michael *et al.* 2014), although medium to longer-term benefits to arboreal and semi-arboreal guilds are predicted based on increases in native vegetation cover (Vesk & Dorrough 2006). We argue that grazing management alone is inadequate to protect and enhance approximately 80% of all reptile species associated with box gum grassy woodland, especially those reliant on old growth and non-renewable resources. Instead, we recommend that future agri-environment schemes place more emphasis on bush rock retention, rocky outcrop restoration and fallen timber management to improve reptile conservation outcomes in agricultural landscapes.

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References

Austin M. (2007) Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecol. Model.* **200**, 1-19.

Benson J. S. (2008) New South Wales Vegetation Classification and Assessment Part 2: Plant communities of the NSW South-western Slopes Bioregion and update of NSW Western Plains plant communities, Version 2 of the NSWVCA database. *Cunninghamia* **10**, 599-672.

Blaum N., Mosner E., Schwager M. & Jeltsch F. (2011) How functional is functional? Ecological groupings in terrestrial animal ecology: towards an animal functional type approach. *Biodivers. Conserv.* **20**, 2333-2345.

Botts E. A., Erasmus B. F. & Alexander G. J. (2013) Small range size and narrow niche breadth predict range contractions in South African frogs. *Global Ecol. Biogeogr*. **22**, 567-576.

BOM (2013) Bureau of Meterology http://www.bom.gov.au/ (accessed on 17 October 2013).

Brown J. H., Mehlman D. W. & Stevens G. C. (1995) Spatial variation in abundance. *Ecology* **76,** 2028-2043.

Brown G. W., Dorrough J. W. & Ramsey D. S. (2011) Landscape and local influences on patterns of reptile occurrence in grazed temperate woodlands of southern Australia. *Landscape Urban Plan*. **103**, 277-288.

Clarke K. R. & Gorley R. N. (2006) *PRIMER v6*. Plymouth Marine Laboratory.

Commonwealth of Australia (2009) *Environmental Stewardship Strategic Framework*. Canberra: Commonwealth of Australia.

Croak B. M., Webb J. K. & Shine R. (2013) The benefits of habitat restoration for rock-dwelling velvet geckos *Oedura lesueurii*. *J. Appl. Ecol.* **50**, 432-439.

Croak B. M., Pike D. A., Webb J. K. & Shine R. (2010) Using artificial rocks to restore nonrenewable shelter sites in human-degraded systems: colonization by fauna. *Restor. Ecol.* **18**, 428-438.

Cunningham R. B., Lindenmayer D. B., Crane M., Michael D. & MacGregor C. (2007) Reptile and arboreal marsupial response to replanted vegetation in agricultural landscapes. *Ecol. Appl*. **17**, 609-619.

Dorrough J., McIntyre S., Brown G., Stol J., Barrett G. & Brown A. (2012) Differential responses of plants, reptiles and birds to grazing management, fertilizer and tree clearing. *Austral Ecol.* **37**, 569-582.

Driscoll D. A. & Lindenmayer D. B. (2012) Framework to improve the application of theory in ecology and conservation. *Ecol. Monogr.* **82**, 129-147.

Driscoll D., Freudenberger D. & Milkovits G. (2000) *Impact and Use of Firewood in Australia*. CSIRO Sustainable Ecosystems, Canberra.

Elton C. S. (1927) *Animal Ecology*. Sidgwick & Jackson, London.

Fischer J., Lindenmayer D. B. & Cowling, A. (2004) The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. *J. Appl. Ecol.* **41**, 32-44.

Fischer J., Stott J., Zerger A., Warren G., Sherren K. & Forrester R. I. (2009) Reversing a tree regeneration crisis in an endangered ecoregion. *P. Natl. Acad. Sci*. **106**, 10386-10391.

Foufopoulos J. & Ives A. R. (1999) Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. *Am. Nat.* **153**, 1-25.

Gehring T. M. & Swihart R. K. (2003) Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. *Biol. Conser.* **109**, 283-295.

Gibbons J. W., Scott D. E., Ryan T. J., Buhlmann K. A., Tuberville T. D., Metts B. S., Greene J. L., Mills T., Leiden Y., Poppy S. & Winnie C. T. (2000) The global decline of reptiles, déjà vu amphibians. *BioScience* **50**, 653-666.

Grinnell J. (1917) The niche-relationships of the California Thrasher. *The Auk*. 427-433.

Hobbs R. J. & Yates C. J. (2000) *Temperate Eucalypt Woodlands in Australia: Biology, Conservation, Management and Restoration*. Surrey Beatty & Sons, Chipping Norton, Sydney.

Holmes R. T., Bonney Jr R. E. & Pacala S. W. (1979) Guild structure of the Hubbard Brook bird community: a multivariate approach. *Ecology* **1979**, 512-520.

Holt R. D. (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *P. Natl. Acad. Sci.* **106**, 19659-19665.

Hutchinson G. E. (1957) Concluding remarks - Cold Spring Harbour Symp. *Quantitative Biol*. **22**, 415–427.

Kay G., Michael D.R., Crane M., Okada S. MacGregor C., Florance D., Trengove D., McBurney L., Blair D. & Lindenmayer D. (2013) A list of reptiles and amphibians from Box-Gum Grassy Woodlands in south-eastern Australia. *Check List* **9**, 476-481.

Kearney M. (2006) Habitat, environment and niche: what are we modelling? *Oikos* **115**, 186-191.

Kornan M., Holmes R. T., Recher H. F., Adamik P. & Kropil R. (2013) Convergence in foraging guild structure of forest breeding bird assemblages across three continents is related to habitat structure and foraging opportunities. *Community Ecol.* **14**, 89-100.

Lee T. M. & Jetz W. (2011) Unravelling the structure of species extinction risk for predictive conservation science. *P. Roy. Soc B-Biol. Sci.*, **278**, 1329-1338.

Leibold M. A. (1995) The niche concept revisited: mechanistic models and community context. *Ecology* **76**, 1371-1382.

Lindenmayer D., Bennett A. & Hobbs R. (Eds.) (2010) *Temperate Woodland Conservation and Management*. CSIRO Publishing, Collingwood, Melbourne.

Lindenmayer D. B., Zammit C., Attwood S. J., Burns E., Shepherd C. L., Kay G. & Wood J. (2012) A novel and cost-effective monitoring approach for outcomes in an Australian biodiversity conservation incentive program. *PLoS One* **7**, e50872. doi:10.1371/journal.pone.0050872

Lunt I. D., Winsemius L. M., McDonald S. P., Morgan J. W. & Dehaan R. L. (2010) How widespread is woody plant encroachment in temperate Australia? Changes in woody vegetation cover in lowland woodland and coastal ecosystems in Victoria from 1989 to 2005. *J. Biogeogr.* **37**, 722-732.

Mac Nally R. (1994). Habitat-specific guild structure of forest birds in south-eastern Australia: a regional scale perspective. *J. Anim. Ecol*. **63**, 988-1001.

Mac Nally R., Parkinson A., Horrocks G., Conole L. & Tzaros C. (2001) Relationships between terrestrial vertebrate diversity, abundance and availability of coarse woody debris on south-eastern Australian floodplains. *Biol. Conser.* **99**, 191-205.

Manning A. D., Cunningham R. B. & Lindenmayer D. B. (2013) Bringing forward the benefits of coarse woody debris in ecosystem recovery under different levels of grazing and vegetation density. *Biol. Conser*. **157**, 204-214.

McGlade J. (Ed.) (2009) *Advanced Ecological Theory: Principles and Applications*. Wiley-Blackwell, Oxford.

McInerny G. J. & Etienne R. S. (2012) Ditch the niche - is the niche a useful concept in ecology or species distribution modelling? *J. Biogeogr.* **39**, 2096-2102.

Michael D. R., Cunningham R. B. & Lindenmayer D. B. (2008) A forgotten habitat? Granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. *J. Appl. Ecol.* **45**, 1742-1752.

Michael D. R., Lindenmayer D. B. & Cunningham R. B. (2010) Managing rock outcrops to improve biodiversity conservation in Australian agricultural landscapes. *Ecol. Manag. Restor.* **11**, 43-50.

Michael D. R., Lindenmayer D. B. & Wood J. (2013) Biodiversity baseline surveys: implications for threatened grassy woodland management in the North East and Goulburn Broken ctachments, Victoria. Report to the North East Catchment Management Authority, Wodonga, Victoria.

Michael D.R., Wood J., Crane M., Montague-Drake R. & Lindenmayer D.B. (2014) How effective are agri-environment schemes for protecting and improving herpetofaunal diversity in Australian endangered woodland ecosystems? *J. Appl. Ecol.* **51**, 494-505.

Owens I. P. E & Bennett P. M. (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *P. Natl. Acad. Sci USA* **97**, 12144-12148.

Peterson A. T. (2011) Ecological niche conservatism: a time structured review of evidence. *J. Biogeogr.* **38**, 817–827.

Pianka E. R. (1973) The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **1973**, 53-74.

Pianka E. R. (1976) Competition and niche theory. In: *Theoretical Ecology: Principles and Applications* (ed R. M. May) pp.114-141. Saunders, Philadelphia.

Pianka E. R. (1980) Guild structure in desert lizards. *Oikos* **1980**, 194-201.

Pike D. A., Croak B. M., Webb J. K. & Shine (2010) Subtle - but easily reversible - anthropogenic disturbance seriously degrades habitat quality for rock-dwelling reptiles. *Anim Conser* **13**, 411-418

Schoener T. W. (1974) Resource partitioning in ecological communities. *Science* **185**, 27-39.

Shine R., Webb J. K., Fitzgerald M. & Sumner J. (1998). The impact of bush-rock removal on an endangered snake species, *Hoplocephalus bungaroides* (Serpentes: Elapidae). *Wildl. Res.* **25**, 285-295.

Thuiller W. (2004) Patterns and uncertainties of species' range shifts under climate change. *Glob. Change Biol*. **10**, 2020-2027.

Turner M. G., Gardner R. H. & O'neill R. V. (2001) *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer Verlag, New York.

Webb J. K. & Shine R. (1999) Paving the way for habitat restoration: can artificial rocks restore degraded habitats of endangered reptiles? *Biol. Conser.* **90**, 93-99.

Wiens J. A. (1995) Landscape mosaics and ecological theory. In: *Mosaic Landscapes and Ecological Processes* (eds L. Hannson, L. Fahrig & G. Merriam) pp. 1-26. Springer, Netherlands.

Whittaker R. H., Levin S. A. & Root R. B. (1973) Niche, habitat, and ecotope. *Am. Nat.* **1973**, 321-338.

Vesk P. A. & Dorrough J. W. (2006) Getting trees on farms the easy way? Lessons from a model of eucalypt regeneration on pastures. *Aust. J. Bot.* **54**, 509-519.

Wong D. T., Jones S. R., Osborne W. S., Brown G. W., Robertson P., Michael D. R. & Kay G. M. (2011) The life history and ecology of the Pink-tailed Worm-lizard *Aprasia parapulchella* Kluge - a review. *Aust. Zool.* **35**, 927-940

Table 1. Biodiversity monitoring programs in the temperate woodland of south-eastern Australia showing the number of survey sites, survey year and survey effort (Literature sources are provided for more information on the experimental design of each program).

Monitoring Program	Number of sites	Year of survey	Survey effort (sites x year)	Literature
South- west Slopes Restoration Study	219	2002, 2003, 2005, 2008, 2011	1095	Cunningham *et al.* 2008
Murray Biodiversity Monitoring Program	93	2008, 2009, 2010, 2012	372	Michael *et al.* 2014
North East/Goulburn Broken Biodiversity Monitoring Program	40	2010, 2011, 2012	120	Michael *et al.* 2013
Environmental Steward Program	325	2010, 2011, 2012	1065	Lindenmayer *et al.* 2012
Total	677		2652	

Table 2. Temperate woodland reptiles observed in this study from south-eastern Australia, showing activity pattern (D = diurnal, N = nocturnal), niche breadth values (*B*) and microhabitat categories (OG: open ground, LL: leaf litter, OL: on log (including fallen trees), OR: on rock (including outcrops), TT: tree trunk (including tree stumps and dead trees), UB: under bark, UL: under log and UR: under surface rock). Species with *B* < 1.5 were classified as habitat specialists and species with *B* > 1.5 were classified as habitat generalists.

Common Name	**Species**	**Number of observations**	***B***	**Microhabitat**
Agamidae				
Burn's Dragon	*Amphibolurus burnsi* (D)	3	1.00	OL
Jacky Dragon	*Amphibolurus muricatus* (D)	10	1.15	OL, OR, TT
Nobby Dragon	*Diporiphora nobbi* (D)	6	2.57	LL,OL,OR,
Eastern Water Dragon	*Intellagama lesueurii* (D)	1	1.00	OL
Eastern Bearded Dragon	*Pogona barbata* (D)	38	3.86	OG,LL,OL,OR,TT,UL
Gekkonidae				
Zig Zag Velvet Gecko	*Amalosia rhombifer* (N)	1	1.00	UB
Southern Marbled Gecko	*Christinus marmoratus* (N)	127	1.59	LL,OR,UB,UL
Eastern Stone Gecko	*Diplodactylus vittatus* (N)	41	1.50	LL,UL,UR
Tree Dtella	*Gehyra variegata* (N)	13	2.25	UB,UL,UR
Binoe's Gecko	*Heteronotia binoei* (N)	15	1.99	UB,UL,UR
Northern Velvet Gecko	*Nebulifer robusta* (N)	4	1.60	UB,UR
Southern Spotted Velvet Gecko	*Oedura tryoni* (N)	2	2.00	UB,UR
Southern Spiny-tailed Gecko	*Strophurus intermedius* (D/N)	26	1.83	UB,UL
Thick-tailed Gecko	*Underwoodisaurus milii* (N)	12	1.18	UL,UR
Pygopodidae				
Pink-tailed Worm Lizard	*Aprasia parapulchella* (D/N)	50	1.00	UR
Olive Legless Lizard	*Delma inornata* (D)	19	2.59	LL,UL,UR
Leaden Delma	*Delma plebeia* (D/N)	6	2.57	LL,UL,UR
Excitable Delma	*Delma tincta* (N)	2	2.00	UL,UR
Burton's Snake Lizard	*Lialis burtonis* (D)	1	1.00	UR
Scincidae				

Two-clawed Worm Skink	*Anomalopus leuckartii* (D)	12	1.80	UL,UR
Southern Rainbow Skink	*Carlia tetradactyla* (D)	114	4.01	OG,LL,OR,UB,UL,UR
Lively Rainbow Skink	*Carlia vivax* (D)	2	1.00	LL
Ragged Snake-eyed Skink	*Cryptoblepharus pannosus* (D)	959	2.41	OG,LL,OL,OR,TT,UB,UL,UR
Elegant Snake-eyed Skink	*Cryptoblepharus pulcher* (D)	46	2.31	OL, TT, UB
Eastern Ctenotus	*Ctenotus orientalis* (D)	2	1.00	UR
Eastern Striped Skink	*Ctenotus robustus* (D)	238	2.27	OG, LL, TT, UL, UR
Copper-tailed Skink	*Ctenotus taeniolatus* (D)	35	1.12	UL, UR
Cunningham's Skink	*Egernia cunninghami* (D)	35	1.41	OL, OR, UB
Tree Crevice Skink	*Egernia striolata* (D)	89	3.13	OL, OR, TT, UB, UR
Eastern Water Skink	*Eulamprus quoyii* (D)	1	1.00	OL
Three-toed Earless Skink	*Hemiergis talbingoensis* (D/N)	119	1.34	LL, UL, UR
Grass Skink	*Lampropholis delicata* (D)	62	3.73	OG, LL, UB, UL, UR
Garden Skink	*Lampropholis guichenoti* (D)	16	3.04	OG, LL, UB, UL, UR
South-eastern Slider	*Lerista bougainvillii* (D)	29	1.42	LL, UL, UR
Timid Slider	*Lerista timida* (D)	64	2.21	LL,UL,UR
White's Skink	*Liopholis whitii* (D)	1	1.00	UR
Litter Skink	*Lygisaurus foliorum* (D)	24	2.79	OG, LL, UL,UR
Grey's Skink	*Menetia greyii* (D)	34	2.82	LL, UL,UR
Boulenger's Skink	*Morethia boulengeri* (D)	1159	2.70	OG, LL, OL, TT, UB, UL, UR
Shingleback	*Tiliqua rugosa* (D)	14	2.18	OG, UL, UR
Common Blue-tongue	*Tiliqua scincoides* (D)	7	1.32	UL, UR
Varanidae				
Lace Monitor	*Varanus varius* (D)	8	1.68	LL, OR, TT
Typhlopidae				
Blackish Blind Snake	*Ramphotyphlops nigrescens* (D/N)	9	1.25	UL, UR
Brown-snouted Blind Snake	*Ramphotyphlops wiedii* (D/N)	12	1.00	UR
Pythonidae				
Inland Carpet Python	*Morelia spilota* (D/N)	1	1.00	OR
Elapidae				
Yellow-faced Whip Snake	*Demansia psammophis* (D)	9	1.97	OG, UL, UR
Red-naped Snake	*Furina diadema* (D/N)	2	2.00	UL,UR
Dwyer's Snake	*Parasuta dwyeri* (D/N)	22	1.72	LL, UL, UR

Red-bellied Black Snake	*Pseudechis porphyriacus* (D)	3	1.80	OG, UR
Eastern Brown Snake	*Pseudonaja textilis* (D)	18	2.41	OG, UL, UR
Curl Snake	*Suta suta* (D/N)	2	1.00	UL
Bandy Bandy	*Vermicella annulata* (D/N)	2	1.00	UR

Table 3. Classification of temperate woodland reptiles in south-eastern Australia based on microhabitat guild membership, mode of thermoregulation and niche affiliation (species with < 2 observations are not included).

Guild	**Niche**	**Species assemblage**
Saxicolous (outcrop-dwelling)	Specialist	*Egernia cunninghami*
	Generalist	*Egernia striolata*
Arboreal (bark-dwelling)	Generalist	*Christinus marmoratus, Gehyra variegata*, *Nebulifer robusta*, *Strophurus intermedius*
Semi-arboreal (tree/log-dwelling)	Specialist	*Amphibolurus burnsi*, *A. muricatus*
	Generalist	*Cryptoblepharus pannosus*, *C. pulcher*, *Diporiphora nobbi*, *Pogona barbata*, *Varanus varius*
Fossorial (log-dwelling)	Specialist	*Hemiergis talbingoensis*, *Ramphotyphlops nigrescens*, *Tiliqua scincoides*
	Generalist	*Anomalopus leuckartii*, *Heteronotia binoei*, *Lerista timida*
Cryptozoic (surface rock-dwelling)	Specialist	*Aprasia parapulchella*, *Ctenotus taeniolatus*, *Diplodactylus vittatus*, *Lerista bougainvillii*, *Ramphotyphlops wiedii*, *Underwoodisaurus milii*
	Generalist	*Ctenotus robustus*, *Demansia psammophis*, *Parasuta dwyeri*, *Pseudechis porphyriacus*
Terrestrial (group 1: open ground)	Generalist	*Tiliqua rugosa*, *Pseudonaja textilis*
Terrestrial (group 2: rock/log/litter-dwelling)	Generalist	*Carlia tetradactyla*, *Lampropholis delicata*, *L. guichenoti*, *Morethia boulengeri*
Terrestrial (group 3: rock/log-dwelling)	Generalist	*Delma inornata*, *D. plebeia*
Terrestrial (group 4: litter-dwelling)	Generalist	*Menetia greyii*, *Lygisaurus foliorum*

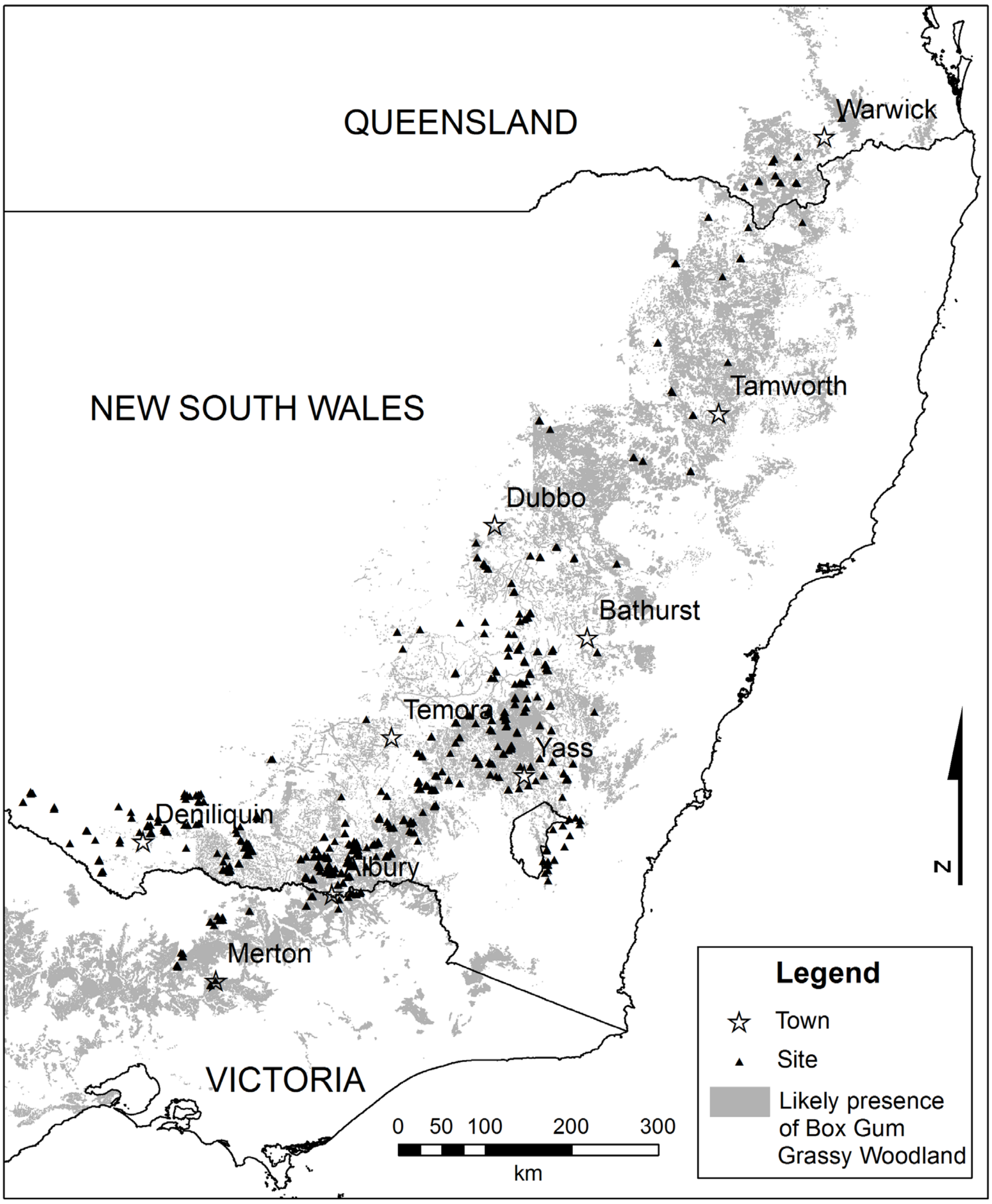


Figure 1. Location of long-term temperate woodland biodiversity monitoring sites (triangles) and the likely extent of box gum grassy woodland in south-eastern Australia.

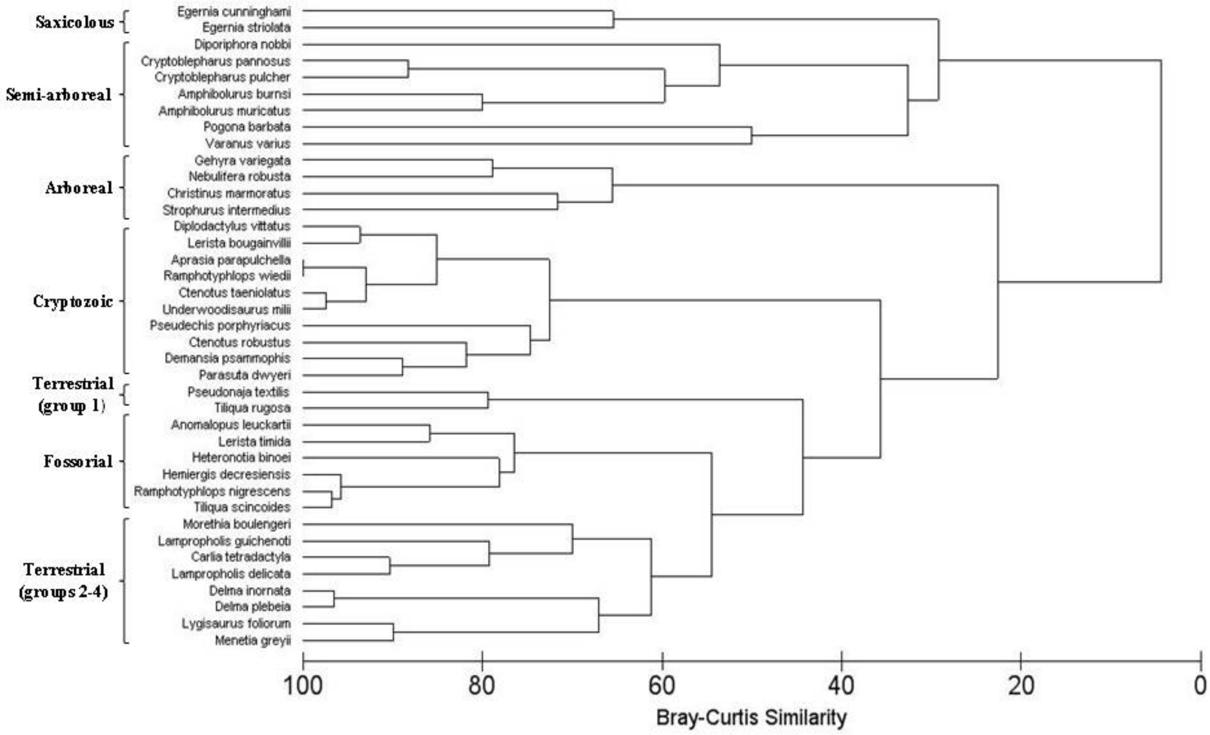
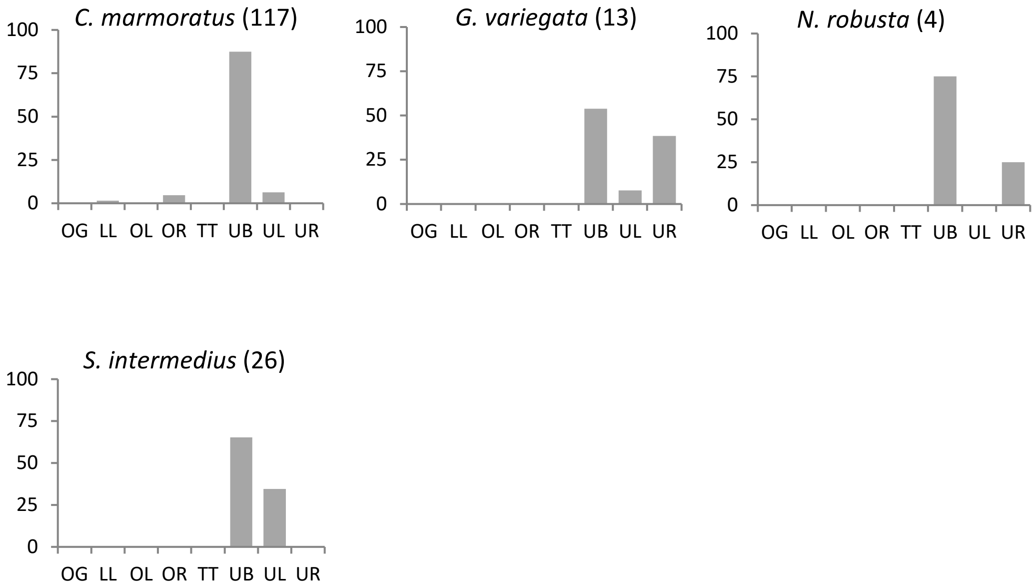
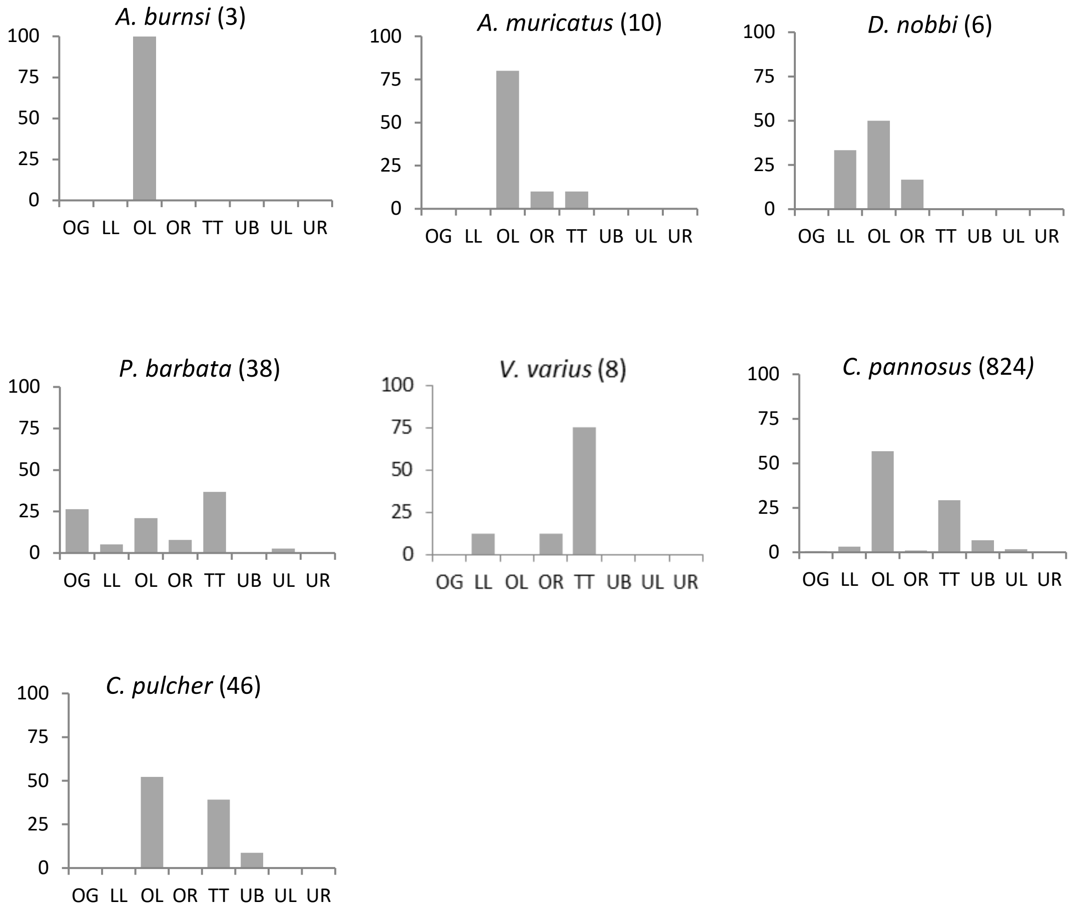


Figure 2. Cluster analysis showing microhabitat relationships among 39 reptile species in the temperate woodlands of south-eastern Australia (Note: excludes species with less than two observations).

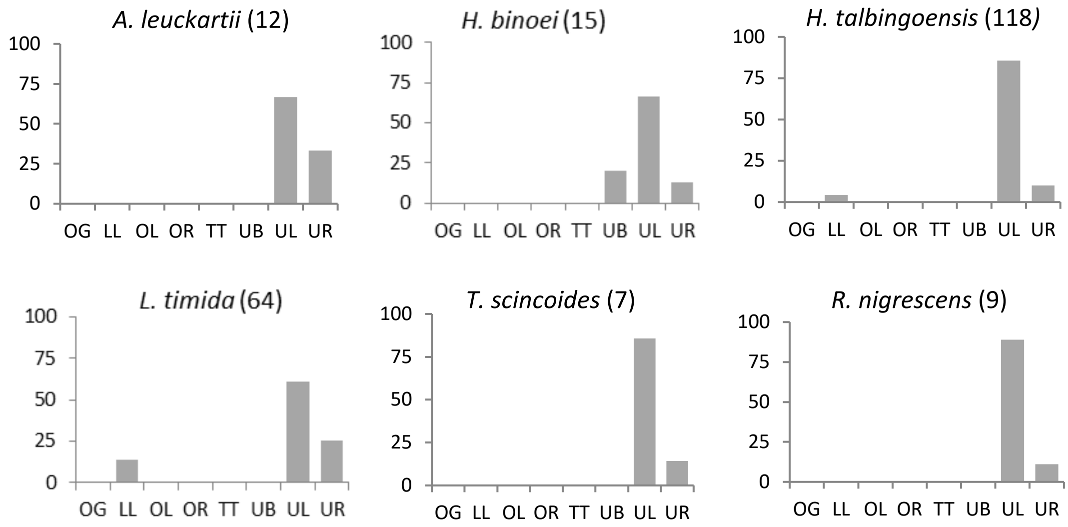
Supporting information



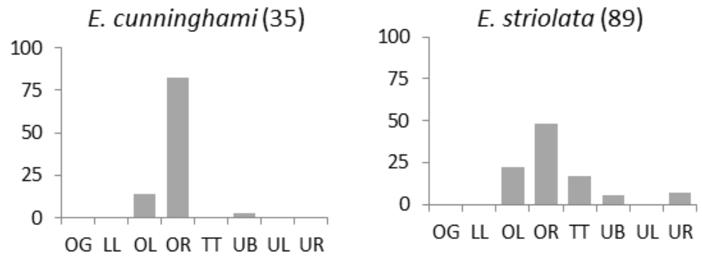
S1. Frequency distribution of arboreal species in the box gum grassy woodland of south-eastern Australia.



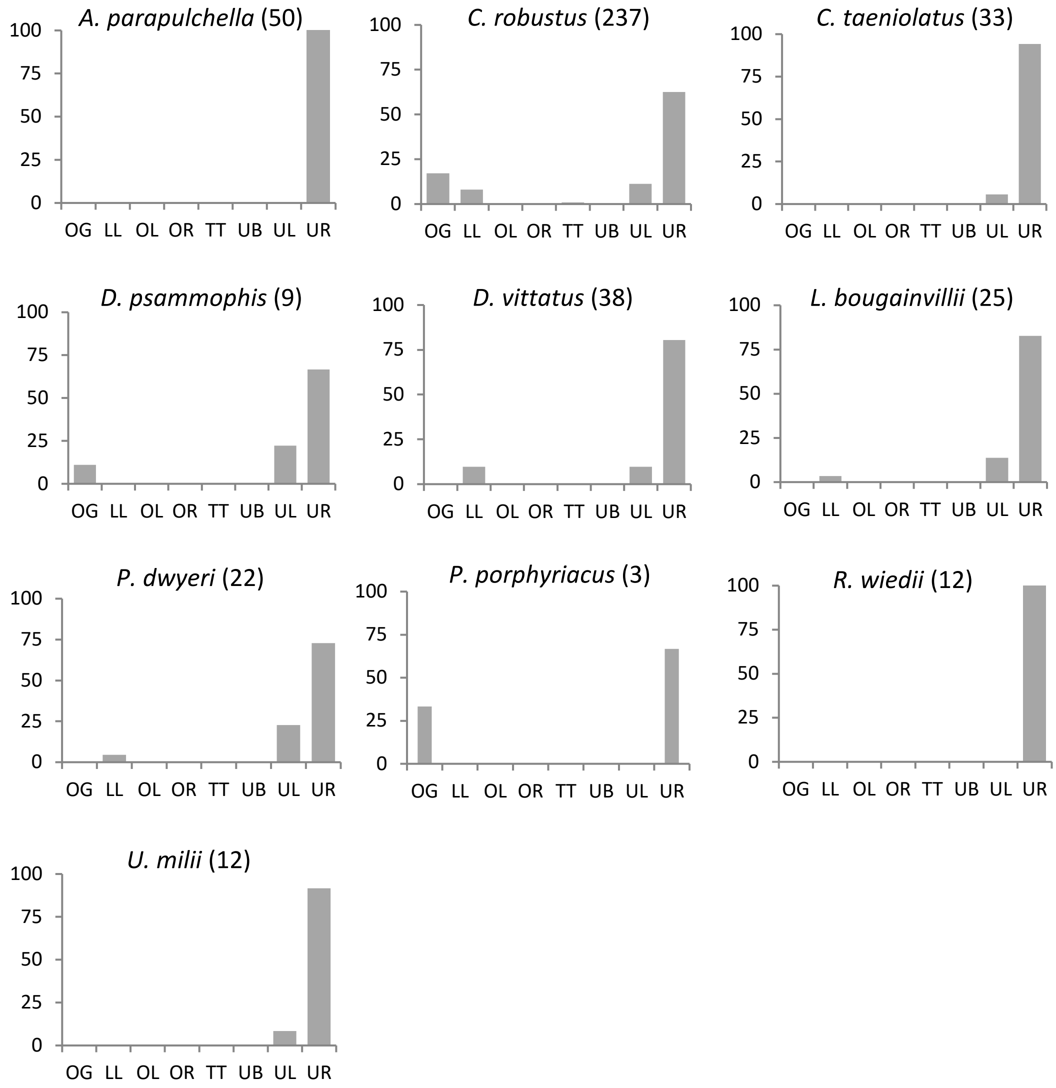
S2. Frequency distribution of semi-arboreal species in the box gum grassy woodland of south-eastern Australia.



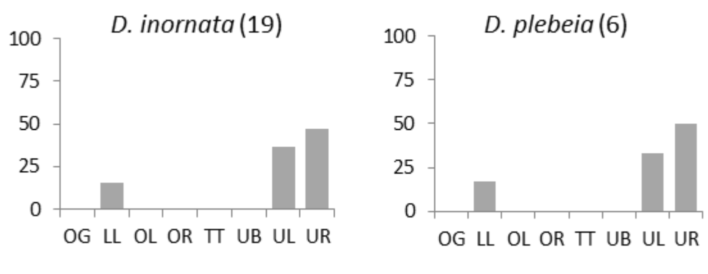
S3. Frequency distribution of fossorial (log-dwelling) species in the box gum grassy woodland of south-eastern Australia.



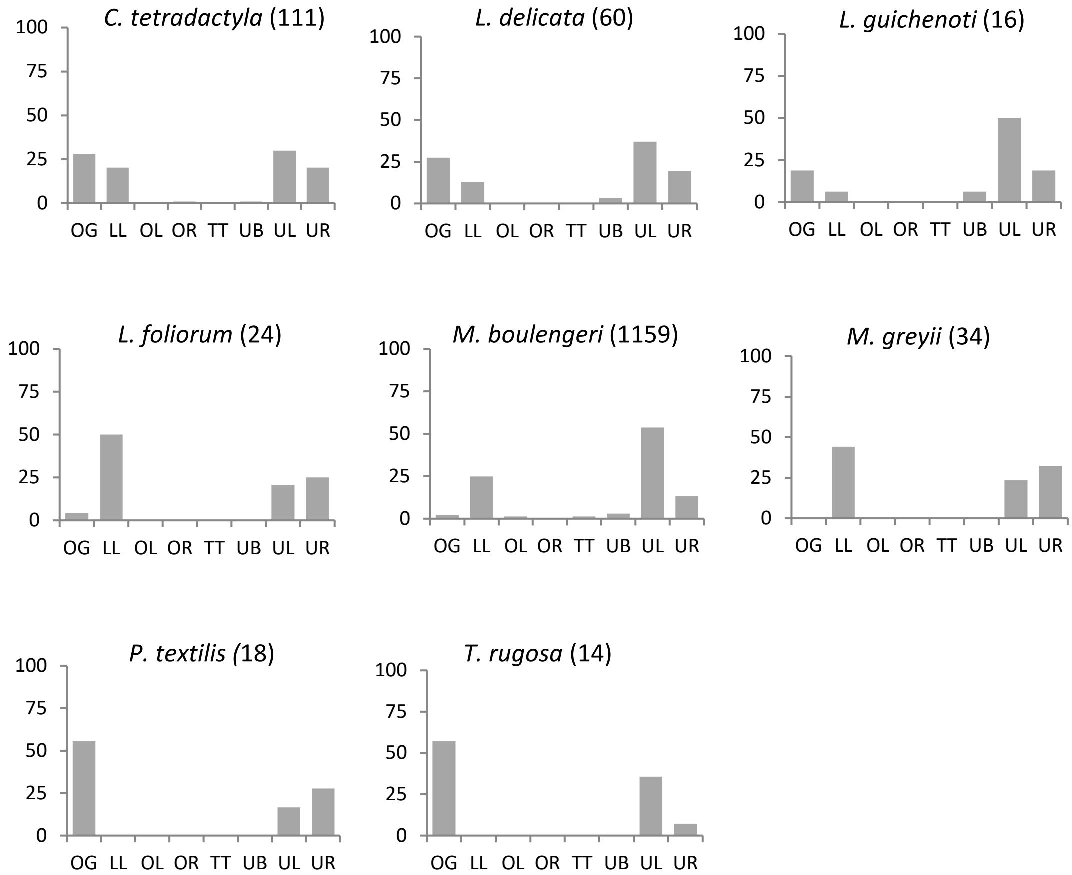
S4. Frequency distribution of saxicolous (rocky outcrop-dwelling) species in the box gum grassy woodland of south-eastern Australia.



S5. Frequency distribution of cryptozoic (rock-dwelling) species in the box gum grassy woodland of south-eastern Australia.



S6. Frequency distribution of log/rock-dwelling species in the box gum grassy woodland of south-eastern Australia.



S7. Frequency distribution of terrestrial species in the box gum grassy woodland of south-eastern Australia.

S8. Example of bush rock removed from a paddock in Victoria. In these images, surface rocks have been placed in piles within the paddock (left) and along the fence line (right). This activity is a key threatening process that affects reptiles in the box gum grassy woodland ecosystem (Photos: J. Michael).