

Vertebrates are poor umbrellas for invertebrates: cross-taxon congruence in an Australian tropical savanna

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Abstract. Invertebrates are commonly ignored in conservation planning due to their vast diversity, difficulties with species identification, a poor understanding of their spatial patterns, and the impracticability of carrying out comprehensive sampling. Conservation planning for fauna is therefore often based on patterns of diversity and distribution of vertebrates, under the assumption that these are representative of animal diversity more generally. Here, we evaluate how well vertebrates act as umbrellas for invertebrate diversity and distribution in a highly diverse tropical savanna landscape, and we investigate the effect of vertebrate sampling intensity (i.e., number of surveys) on congruence results. We assessed congruence between each of the four classes of terrestrial vertebrates (amphibians, reptiles, birds, and mammals) and twelve invertebrate families (representing four dominant invertebrate taxa: ants, beetles, flies, and spiders) by applying a range of modeling approaches to analyze patterns of cross-taxon congruence in species richness and composition across sampling sites. To investigate drivers of congruence, we applied generalized and distance-based linear models to identify environmental associations of richness and composition for each taxon, then examined variation in environmental associations across taxa. Vertebrate and invertebrate richness was weakly (<30%) associated, and ~60% of the significant associations were negative. Correlations in species composition between vertebrate and invertebrate taxa were also weak, with a maximum of 13% congruence. In most cases, pairwise correlation scores using data from single surveys of vertebrates were only marginally lower than those from multiple surveys. Poor among-site congruence between vertebrates and invertebrates was reflected by marked variation among taxa in their environmental associations. Our findings show that vertebrates are poor umbrellas for invertebrates in the tropical savannas of northern Australia in terms of geographic patterns of diversity and distribution and that this is not just an artifact of low vertebrate sampling intensity. Our study is one of the most comprehensive regional analyses of the congruence of vertebrate and invertebrate diversity, and it significantly adds to the growing evidence that empirical data on invertebrate diversity and distribution are required for conservation planning that effectively protects all faunal diversity.

Key words: conservation planning; environmental associations; faunal survey; sampling intensity; species diversity; surrogate taxa.

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INTRODUCTION

Invertebrates dominate faunal diversity in almost every terrestrial, freshwater, and marine habitat. They are vital to the health and stability of biological communities, due to their involvement in crucial ecological processes such as nutrient cycling, decomposition, pollination, plant productivity, and population control via predation and parasitism (Wilson 1988, Durrant 2009). Given that an estimated 80% of invertebrates are yet to be discovered (Stork 2018), current knowledge of invertebrate diversity and distribution, and of the processes that influence them, is poor (Wilson 1987, Ødegaard 2000, Osborn 2010). The need to improve our understanding of invertebrate diversity and distribution and its key drivers is becoming increasingly urgent as species loss accelerates under the current global extinction crisis, much of which involves unknown invertebrates (Dunn 2005, Régnier et al. 2015, Leather 2018, Eisenhauer et al. 2019).

Despite their importance, invertebrates are often overlooked in faunal surveys for informing conservation planning, owing in a large part to their extreme taxonomic and biological diversity that makes comprehensive surveys impracticable (New 1999, Cardoso et al. 2011, Braby and Williams 2016, Braby 2017). Land managers often rely on the notion that areas designed to protect species of greatest conservation priority (i.e., vertebrates or plants) are simultaneously conserving co-occurring species—the umbrella species concept (Noss 1990, Roberge and Angelstam 2004). Faunal surveys therefore typically focus on vertebrates, with the implicit assumption that patterns of vertebrate diversity and distribution represent those of faunal diversity more generally (Murphy and Wilcox 1986, Landres et al. 1988, Oliver et al. 1998). However, studies that have assessed the use of vertebrates as umbrellas for invertebrates have demonstrated either limited (Murphy and Wilcox 1986, Martikainen et al. 1998, Fleishman et al. 2001) or no (Kerr 1997, French 1999, Rubinoff 2001, Schuldt and Assmann 2010, Jenkins et al. 2013) support for this assumption.

The lack of congruence between vertebrates and invertebrates is commonly attributed to their contrasting responses to environmental variation (Ricketts et al. 2002, Heino et al. 2005, 2009). However, another factor contributing to low

congruence may be insufficient sampling intensity, leading to data that may not adequately represent the biological communities of interest (see de Solla et al. 2005). Detectability of species occurrence during faunal surveys is rarely perfect, with many species not recorded at sites where they actually occur. Failure to account for imperfect detectability can bias commonly used metrics of occurrence and richness and hence contribute to inaccurate study conclusions and uncertainty in management and policy decisions (Driscoll 2010, Ruiz-Gutiérrez and Zipkin 2011, Kellner and Swihart 2014). The best way to address the problems associated with low species detectability is to increase sampling intensity to generate more robust data for comparison, by maximizing chances of recording species occupancy. However, the effect of increased survey effort on the outcome of congruence analyses is largely unexplored.

There is a pressing need for further assessment of the efficacy of the vertebrate-umbrella approach in conservation planning, especially in highly diverse biomes such as the tropics, which continue to receive far less attention in biodiversity research than do temperate regions (Tittley et al. 2017). Moreover, such analyses need to move beyond the simple question of whether geographic patterns of vertebrate diversity are correlated with those of invertebrates, by addressing the critical issue of whether such correlations are strong enough to make vertebrates reliable umbrellas for invertebrates in conservation planning. For example, it has been suggested that one taxon can only be a reasonable surrogate of another if it has a predictive capacity of at least 60% (Leal et al. 2010), and predictive thresholds of 75% (Lovell et al. 2007) and 80% (Fleishman et al. 2005) have been proposed for effective surrogacy. As far as we are aware, the only examples where a vertebrate taxon has been shown to have even close to such predictive capacity for a diverse invertebrate group involve birds and butterflies—bird and butterfly species richness were found to be highly (74%) correlated across six closely situated sites representing a gradient of urban land use in California (Blair 1999); six bird species could be used to explain 55% of deviance in butterfly richness across three adjacent mountain ranges in North America's central Great Basin (Fleishman et al. 2005); and

bird and butterfly composition was shown to be 44% congruent in montane meadow habitats across the Greater Yellowstone region (Su et al. 2004).

In this study, we evaluate the effectiveness of vertebrates as umbrellas for the diversity and distribution of terrestrial invertebrates across 78 sites in the tropical savannas of northern Australia. We consider all four classes of terrestrial vertebrates (amphibians, reptiles, birds, and mammals) and 12 families representing four dominant invertebrate taxa: Formicidae (ants); Carabidae, Curculionidae, Ptinidae, Scarabaeidae, Staphylinidae, Tenebrionidae (beetles); Chloropidae, Phoridae (flies); and Lycosidae, Salticidae, Zodariidae (spiders). Specifically, we aim to (1) assess the level of congruence between vertebrate and invertebrate taxa in among-site patterns of species richness and composition, (2) gauge the effect of vertebrate sampling intensity on the level of congruence, and (3) examine variation in environmental associations of community richness and composition between vertebrate and invertebrate taxa, as a means of accounting for the observed levels of cross-taxon congruence.

METHODS

Study sites

This study was based on data collected from 78 long-term monitoring sites of the Three Parks Savanna Fire-Effects Plot Network (part of Australia's previous Long Term Ecological Research Network [LTERN]; <http://www.ltern.org.au/>) in contiguous Kakadu (32 sites) and Nitmiluk (46 sites) National Parks in the tropical savannas of northern Australia (Fig. 1). The Parks encompass three major landscape units: lowland savanna woodlands; sandstone country of the western Arnhem Land and Marrawal Plateau; and floodplains associated with major river systems (Finlayson and von Oertzen 2012). The climate is tropical monsoonal, with high (typically 30–40°C) maximum temperatures throughout the year and rainfall heavily concentrated into a summer wet season of November–April (Andersen 2000). There is a gradient in mean annual rainfall from about 1440 mm in the north to 1080 mm in the south of the contiguous parks, over a distance of ~300 km. Collectively, the two

parks comprise the largest area of contiguous conservation estate in northern Australia, a combined area of 22,013 km². Despite supporting an extremely diverse biota with exceptionally high conservation values (Press et al. 1995, Woinarski et al. 2007, Winderlich and Woinarski 2014), Kakadu's invertebrate fauna has received little survey attention, restricted to limited sampling of butterflies (Kikkawa and Monteith 1980), ants (Andersen 1991, 1993), grasshoppers (Andersen et al. 2000), and termites (Braithwaite et al. 1988). There have been no systematic surveys of any invertebrate group in Nitmiluk.

Vertebrate data

Surveys of terrestrial vertebrates have been conducted at the sites every five years since 1996, involving two to three days/nights of live-trapping and repeated diurnal and nocturnal timed-area searches for birds, reptiles, and amphibians, in a 50 × 50 m quadrat. Live-trapping involved baited Elliot and cage traps for small mammals and 20-Liter bucket pitfall traps and associated drift fences for small mammals, amphibians, and reptiles (see Woinarski et al. 2010 for details). We used vertebrate data collected at Kakadu sites in 2004, 2009, and 2014 and at Nitmiluk sites in 2005, 2011, and 2015. We pooled capture data across all three sessions to provide a more robust metric of vertebrate diversity at the sites, due to low detectability of species in any one survey session. We acknowledge that such pooling of data risks inflating measures of site-level diversity (because previously recorded species may no longer be occupying the site at the time of subsequent surveys), but we see this risk to obtaining robust measures of site diversity as being considerably lower than that due to low species detectability. The data comprise records of a total of 311 vertebrate species (Table 1; for list of species see Data S1).

Invertebrate data

Terrestrial invertebrates were sampled during the vertebrate sampling at Kakadu in 2014 (February–April) and at Nitmiluk in 2015 (April–May). Sampling was conducted using pitfall traps, a standard method for trapping ground-dwelling invertebrates (Southwood 1978, Bestelmeyer et al. 2000, Skvarla et al. 2016) that could be readily included in the existing faunal survey.

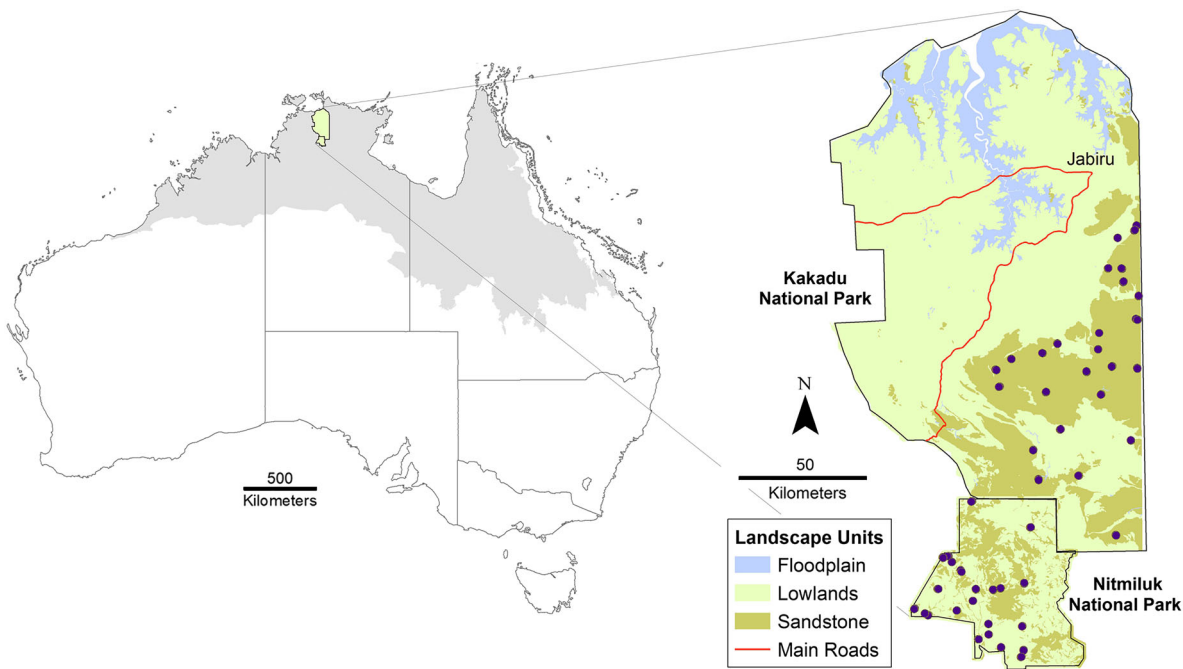


Fig. 1. Location of 78 sites (each point represents paired sites located 100–800 m apart) within Kakadu National Park and Nitmiluk National Park, and position of the parks in Australia's tropical savanna region (shaded in gray).

Two sets of invertebrate-specific pitfall traps were used: A 40×10 m grid of ten cup-sized (65 mm diameter) traps and a 40×30 m grid of twenty smaller specimen container-sized (45 mm diameter) traps, with all traps set at 10-m intervals. Traps were $\frac{3}{4}$ filled with ethylene glycol, buried in the ground flush with the soil surface, and collected after 48 h. Invertebrate by-catch captured in three 20-L vertebrate bucket traps was also collected each morning and afternoon. Capture data from all traps were pooled to provide total abundance data for all species for each site. Invertebrates had not been previously sampled at the sites, so our data are from a single trapping session only. Details of trapping layout and an overview of catches are provided in Oberprieler et al. (2019). Twelve invertebrate families were targeted for analysis, based on their high abundance and diversity in traps, taxonomic tractability, and broad representation of functional diversity: Formicidae (ants); Carabidae, Staphylinidae, Curculionidae, Scarabaeidae, Tenebrionidae, and Ptinidae (beetles); Chloropidae and Phoridae (flies); and Lycosidae,

Salticidae, and Zodariidae (spiders). A total of 668 species from these families were sampled across all three trap arrays (Table 2; for list of species see Data S1). We consider these taxa at the level of family rather than order to provide a finer-grained perspective on invertebrate distribution, and to avoid the potential masking of important patterns by lumping distributions of ecologically diverse groups.

Environmental variables

We collated data on 18 environmental variables (for description of variables; see Appendix S1: Table S1, and for data, see Data S1) to assess variation in environmental associations of community richness and composition between vertebrate and invertebrate taxa. Fifteen of these variables were collected at the sites during the 2014–2015 surveys: percent cover of grass (perennial tussock, annual tussock, and hummock), sedges, canopy, rock, litter, bare ground, other ground cover; number of logs >5 cm; rock type; soil composition (color, depth, and texture); and elevation. Using ArcGIS 9.0 (Esri, Redlands,

Table 1. Vertebrate taxa and their total number of species recorded from faunal survey at 78 sites in Kakadu and Nitmiluk National Parks between 2004 and 2015.

Taxon	Common name	Total species
Amphibia	Frogs	29
Hylidae	Tree frogs	15
Myobatrachidae	Froglets	13
Microhylidae	Narrow-mouthed frogs	1
Aves	Birds	143
Passeriformes	Perching birds	71
Accipitriformes	Hawks, eagles, ospreys, and kites	13
Psittaciformes	Parrots	10
Columbiformes	Pigeons and doves	9
Cuculiformes	Cuckoos	7
Coraciiformes	Kingfishers	6
Galliformes	Turkeys, fowls, and quails	5
Strigiformes	Owls	4
Falconiformes	Falcons	4
Anseriformes	Geese and ducks	4
Charadriiformes	Shorebirds	3
Caprimulgiformes	Nightjars	3
Pelecaniformes	Waterbirds	2
Gruiformes	Cranes and rails	1
Otidiformes	Bustards	1
Mammalia	Mammals	39
Chiroptera	Bats	11
Diprotodontia	Kangaroos, wallabies, wombats, and possums	10
Rodentia	Mice and rats	9
Dasyuomorpha	Carnivorous marsupials	6
Monotremata	Echidnas and platypus	1
Peramelemorpha	Bandicoots and bilbies	1
Carnivora	Dingo	1
Reptilia	Reptiles	100
Scincidae	Skinks	42
Gekkonidae	Geckos	13
Varanidae	Monitor lizards	9
Agamidae	Dragon lizards	7
Elapidae	Elapid snakes	7
Typhlopidae	Blind snakes	6
Pygopodidae	Legless lizards	5
Colubridae	Colubrid snakes	4
Pythonidae	Python snakes	3
Diplodactylidae	Australasian geckos	3
Carphodactylidae	Southern padless geckos	1
Total		311

California, USA), mean annual rainfall for each site was extracted from a 1-km² raster sourced from the WorldClim database <http://www.worldclim.org/> (Hijmans et al. 2005). Fire severity and frequency data were collected by

Table 2. Invertebrate taxa and their total number of species recorded from faunal survey at 78 sites in Kakadu and Nitmiluk National Parks between 2014 and 2015.

Taxon	Common name	Total species
Formicidae	Ants	320
Coleoptera	Beetles	198
Carabidae	Ground beetles	62
Staphylinidae	Rove beetles	54
Curculionidae	Weevils	28
Scarabaeidae	Scarab beetles	29
Tenebrionidae	Darkling beetles	18
Ptinidae	Spider beetles	7
Diptera	Flies	61
Phoridae	Scuttle flies	35
Chloropidae	Grass flies	26
Araneae	Spiders	89
Salticidae	Jumping spiders	39
Zodariidae	Ant-eating spiders	30
Lycosidae	Wolf spiders	20
Total		668

park rangers by visiting the sites once or twice per year and sourced through the LTERN data portal (<https://www.ltern.org.au/knb/>) from databases compiled by Russell-Smith (2017).

Data analysis

Congruence in geographic patterns.—We used generalized linear models (GLMs) to assess the relationship between richness of the 12 invertebrate taxa (response variable) and richness of amphibians, reptiles, birds, and mammals (predictor variables), or any combination of these taxa. Relationships were also assessed between richness of all invertebrates (pooled taxa) and all vertebrates (pooled taxa). Predictor variables were pairwise assessed for co-linearity, but no two variables exceeded a correlation of Pearson $R = 0.3$. Gaussian, Poisson, and negative binomial error distributions were applied to each model and dispersion scores compared to identify the most appropriate error distribution. Due to the excess of zeros for some invertebrate taxa counts, zero-inflated models with Poisson and negative binomial count error distributions were also considered, but these performed poorly compared with negative binomial error distributions. In each case, the best-fitting model was then assessed for non-linearity by applying cubic

and quadratic terms to the predictor variables (four vertebrate classes), but these terms were only retained if they improved model performance. For all models, all four vertebrate classes were included in a full model and terms removed until a minimum adequate model was determined following Crawley (1993). The order of deletion of terms was determined from chi-square tests for full models and reduced models in which only that single term had been deleted. Final models were selected to minimize the Akaike Information Criteria (AIC) value, which, in some cases, required the inclusion of non-significant predictors. When models were similar (i.e., had relatively close AIC values ≤ 2), model deviance of nested models was compared using likelihood ratio tests dependent on the model error structure (Zuur et al. 2009). If there was no significant difference between similar models, the simpler model was selected. Selected final models were validated by visual inspection of residual plots, normal quantile–quantile plots, and residuals/leverage plots. All analyses were conducted in the statistical programming language R v3.3.3 (R Core Team 2013) using the *pscl* (Zeileis et al. 2008), *MASS* (Venables and Ripley 2002), and *lmtree* (Zeileis and Hothorn 2002) packages.

We used Mantel tests to assess how among-site variation in the composition of invertebrate taxa was related to the composition of each of the amphibian, reptile, bird, and mammal communities. To do this, we constructed a resemblance matrix across all sites for each taxon in *PRIMER-E 7.0* (Clarke and Gorley 2015) by calculating Bray–Curtis similarity measures based on square-root transformed abundance data. The transformation evens out the abundance of species, so that similarities are not so strongly driven by highly abundant species. The Bray–Curtis coefficients were zero-adjusted so that they were less erratic for samples with few individuals and were calculable for samples with complete absences. This was done by constructing the Bray–Curtis matrices against a dummy value of 1, which adds a pseudo-species at sites from which no species were recorded (Clarke et al. 2006). Congruence between vertebrate and invertebrate taxa was then assessed by applying pairwise correlations between the Bray–Curtis resemblance matrices using the *RELATE* function

(a non-parametric form of Mantel test) with Spearman's rank method (999 randomized permutations).

Effects of sampling intensity.—To evaluate the effect of sampling intensity on congruence results, we repeated the composition analysis described above using only the vertebrate data collected during the single invertebrate survey session (2014–2015). The single 2014–2015 survey detected 83%, 76%, 77%, and 41%, respectively, of the total amphibian, reptile, bird, and mammal species recorded when pooling across three survey sessions. We were not able to test the effect of sampling intensity on the invertebrate data because there were no previous invertebrate surveys. However, if low detectability was the cause of poor congruence, then congruence would be expected to be improved by increasing detectability of one of the two groups.

Environmental associations.—We used GLMs to identify which environmental variables were contributing to geographic patterns of invertebrate and vertebrate species richness. We ran 16 models (12 invertebrate and 4 vertebrate taxa as response variables), each considering our 18 environmental predictor variables (see Appendix S1: Table S1). We ran three additional models with the response variables total invertebrates, total vertebrates, and total species (invertebrates and vertebrates combined). The modeling procedure was the same as that described above.

We used distance-based linear models (*DistLM*) in *PERMANOVA+* of *PRIMER-E 7.0* (Clarke and Gorley 2015) to determine the environmental variables contributing to site variation in species composition for each of the invertebrate and vertebrate taxa. *DistLM* uses a multiple regression procedure to relate a set of explanatory variables (we used all 18 listed in Appendix S1: Table S1) to a resemblance matrix of species composition. Prior to analyses, all response and predictor variables were square-root transformed so that they were normally distributed—a prerequisite of the analysis approach. A Bray–Curtis resemblance matrix was calculated for each taxon (as described above). All environmental variables were assessed for collinearity using Draftsman plots, but none exceeded a Pearson correlation $R = 0.4$, and therefore, all were included in the models. Marginal tests (999 permutations) were performed to determine the explanatory power

Table 3. Results from GLM analysis showing strength of relationship (coefficient estimate) in species richness between each invertebrate family and the four vertebrate classes (covariates).

Invertebrates	Model	Intercept	Amphibians	Birds	Mammals	Reptiles	Percentage of dev.	Model	Intercept	Total vertebrates	Percentage of dev.
Carabidae	NB	1.41		0.03*		-0.18***	22.69	NB	1.02	-0.012	0.91
Chloropidae	NB	0.75	-0.06*	0.04*		-0.07**	16.82	NB	0.06	0.002	0.05
Curculionidae	NB	-0.29		0.03*	-0.21**		11.83	NB	-0.07	0.002	0.02
Formicidae	NB	3.26	-0.05***	0.02***	-0.04		24.44	NB	3.29	0.003	0.59
Lycosidae	NB	-0.77	0.15**		-0.39*		16.37	NB	-1.09	0.01	0.49
Phoridae	NB	-0.24	-0.08*	0.06***	-0.14*		28.13	NB	0.06	0.02	1.30
Ptinidae	NB	-2.07		0.05	-0.35		12.75	P	-2.04	0.01	0.87
Salticidae	NB	0.58	-0.04	0.004	0.03	-0.003	1.98	P	0.62	-0.002	0.05
Scarabaeidae	P	-0.90	0.07	0.03		-0.09*	11.70	P	-1.69	0.03	4.14
Staphylinidae	NB	1.38				-0.11**	10.55	NB	0.90	-0.015	1.83
Tenebrionidae	P	-2.21		0.07***			15.78	P	-2.10	0.04**	8.70
Zodariidae	NB	-0.69		-0.01	-0.03	0.04	0.92	NB	-0.27	-0.0003	0.00
Total invertebrates	NB	3.55	-0.04**	0.02***	-0.06**		30.86	NB	3.64	0.003	0.68

Notes: The best-fitting model is indicated by NB, negative binomial; P, Poisson. Degrees of freedom for all models are 77. Empty cells indicate cases where covariates (vertebrates) were dropped to improve model fit.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

of each environmental variable on the assemblage structure of each taxon. A stepwise selection procedure was applied and AIC calculated to find the most parsimonious model, that is, the best combination of environmental variables that explained the greatest variation in assemblage structure.

RESULTS

Congruence in geographic patterns

Cross-taxon richness modeling revealed that no combination of vertebrate taxa explained >28% of the among-site variation in species richness of any of the 12 invertebrate families (Table 3). For Staphylinidae, only reptiles were retained as a predictor in the best model, with a negative association that explained ~10% of variation in richness. For Tenebrionidae, only birds were retained in the best model, with a positive association that explained ~15% of variation in richness. In the remaining ten invertebrate models, multiple vertebrate taxa were retained as predictors. For Salticidae, all four vertebrate taxa were retained, but this model performed poorly (<2% deviance explained). Birds were the most common predictor of invertebrate richness, retained in the best model for 10 of 12 invertebrate taxa (Table 3). Bird relationships were largely positive, but all were very weak (coefficient

estimate ≤ 0.07). In contrast, most significant relationships involving other vertebrate taxa were negative; the strongest of these were between mammals and Lycosidae (-0.39) and between mammals and Curculionidae (-0.21; Table 3).

Total invertebrate richness was related to amphibian and mammal richness negatively and to bird richness positively, with the best model explaining ~30% of the observed variation in total invertebrate richness. Total vertebrate richness was a poor predictor of total invertebrate richness and a poor predictor of the richness of all individual invertebrate taxa. Only for Tenebrionidae was there a significant relationship with richness of total vertebrates, but this was very weak (0.04; Table 3).

Cross-taxon modeling of species composition revealed that invertebrate and vertebrate taxa were significantly correlated in 18 of the 48 pairwise relations, and in all cases, the correlations were positive (Table 4). All significant relationships were relatively weak, however, with none exceeding $\rho = 0.28$. The number of significant correlations per vertebrate taxon ranged from one invertebrate family for mammals to six for reptiles. No vertebrate taxon was significantly correlated with Ptinidae, Scarabaeidae, Tenebrionidae, or Zodariidae. Correlations with total invertebrates were significantly positive for all vertebrate taxa, ranging from $\rho = 0.19$ for

Table 4. Spearman’s rank correlations (ρ) between species composition (Bray–Curtis dissimilarity) of vertebrate and invertebrate taxa using vertebrate data from all survey years (2004–2015) and vertebrate data from only the invertebrate survey years (2014–2015).

	Amphibians		Birds		Mammals		Reptiles		Total vertebrates	
	2004–2015 (29)	2014–2015 (24)	2004–2015 (143)	2014–2015 (110)	2004–2015 (39)	2014–2015 (16)	2004–2015 (100)	2014–2015 (76)	2004–2015 (311)	2014–2015 (226)
Carabidae (62)	0.09*	0.17*	0.11	–0.05	–0.09	–0.03	0.27***	0.06	0.17**	–0.003
Chloropidae (26)	0.05	0.06	0.09*	0.05	0.03	–0.05	0.07	0.04	0.09*	0.04
Curculionidae (28)	0.09**	–0.03	0.03	0.01	–0.12	–0.13	0.22***	0.10*	0.09	0.03
Formicidae (320)	0.23***	0.25***	0.29***	0.25***	0.18**	0.07	0.23***	0.12**	0.34***	0.28***
Lycosidae (20)	0.09*	0.22*	0.01	0.03	–0.09	–0.16	0.05	–0.02	0.05	0.05
Phoridae (35)	0.20*	0.02	0.15**	0.09*	–0.08	–0.02	0.22***	0.13**	0.19***	0.08*
Ptinidae (7)	–0.03	–0.17	–0.04	–0.01	–0.14	0.01	0.007	0.07	–0.04	–0.05
Salticidae (39)	0.07*	0.01	0.14**	0.09*	0.08	0.07	0.13*	0.16***	0.18*	0.11**
Scarabaeidae (29)	0.09	0.21*	0.02	–0.13	0.04	–0.04	0.04	–0.02	0.03	–0.11
Staphylinidae (54)	0.08	0.24**	0.22**	0.02	–0.09	–0.08	0.28**	0.10*	0.28***	0.06
Tenebrionidae (18)	0.007	–0.17	–0.06	0.03	–0.01	0.06	0.04	0.06	–0.08	0.01
Zodariidae (30)	0.07	0.1	–0.01	0.05	0.01	–0.15	–0.14	–0.13	–0.02	0.04
Total invertebrates (668)	0.26***	0.29***	0.30***	0.27***	0.19**	0.08	0.24***	0.12**	0.36***	0.32***

Notes: Significance levels determined using non-parametric Mantel test with 999 permutations: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Number of species used in analyses is given in parentheses.

mammals to $\rho = 0.30$ for birds (Table 4). In contrast to species richness, composition correlations involving total vertebrates tended to be higher than for separate taxa. The correlation between total invertebrates and total vertebrates was $\rho = 0.36$ (Table 4).

Effects of sampling intensity

Compared with the single-survey session (2014–2015; total of 226 species), species composition data from multiple vertebrate surveys (2004–2015; total of 311 species) increased the number of significant correlations with invertebrates for all four vertebrate taxa (amphibians and reptiles from 5 to 6, birds 3 to 5, and mammals 0 to 1) and for total vertebrates (from 3 to 6; Table 4). However, for most pairs of vertebrate–invertebrate groups, data from multiple surveys led to no or negligible increases in correlation strength. Only for amphibians did the single-survey data show marginally higher correlations for some (5 of 12) invertebrate taxa, but the strength of these was still low (maximum $\rho = 0.25$; Table 4).

Environmental associations

Environmental associations of species richness were highly variable among the invertebrate taxa

(Table 5–7). Rainfall was the most common associate of richness, with increased richness for four taxa (Lycosidae, Phoridae, Ptinidae, and Tenebrionidae) and decreased richness for three (Salticidae, Staphylinidae, and Zodariidae) at higher rainfall sites (Table 6). Rock cover was also a common environmental associate for invertebrates, with richness of five taxa (Carabidae, Chloropidae, Curculionidae, Lycosidae, and Staphylinidae) decreasing in more rocky areas (Table 5). No other environmental covariate was significantly associated with the richness of more than two of the 12 taxa. Environmental associations of richness also varied markedly among the vertebrate taxa, and these tended to be very different from those of invertebrates. Birds were the only vertebrate taxon for which richness was significantly related to rainfall (Table 6). Of all vertebrates, only reptile richness was related to rock cover, with increased richness in more rocky areas rather than the prevailing negative relationships for invertebrates (Table 5). Mammal richness was significantly associated with soil texture, and among invertebrates, this was also the case for Curculionidae and Zodariidae; however, these relationships were opposite (Table 7). When all invertebrate and vertebrate species were combined (total species), the key predictors

Table 5. Environmental associations of invertebrate and vertebrate species richness, showing strength of relationship of vegetative and ground cover covariates (remaining environmental covariates shown in Tables 6, 7).

Taxon	Percent cover								
	Bare ground	Rock	Litter	Hummock grass	Perennial grass	Annual grass	Sedge	Other ground	Canopy
Invertebrates									
Carabidae		<i>-0.02*</i>		<i>-0.05**</i>					
Chloropidae		<i>-0.02***</i>				0.01			
Curculionidae		<i>-0.02**</i>							
Formicidae									0.002
Lycosidae		<i>-0.03*</i>			<i>-0.03</i>			0.05*	
Phoridae			0.01		0.02*	0.02*			
Ptinidae									
Salticidae	<i>-0.003</i>								
Scarabaeidae	0.03*						0.05**	0.05*	0.02***
Staphylinidae		<i>-0.02*</i>							
Tenebrionidae									0.01*
Zodariidae									
Vertebrates									
Amphibians				0.01			0.02		
Birds								0.02**	0.005**
Mammals			0.01*						
Reptiles		0.009***		0.01**	0.006*	0.006*		0.01*	
Total									
Invertebrates		<i>-0.004*</i>							
Vertebrates				0.005*				0.01***	0.004***
Species		<i>-0.003**</i>							

Notes: Positive associations are indicated in bold and negative associations in italics. For GLM model statistics, see Appendix S1: Table S2, and for description of environmental variables, see Appendix S1: Table S1.
 * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

(percent rock cover and rainfall) matched those of the model including only invertebrates (Tables 5, 6) and explained 26.7% of deviance (Appendix S1: Table S2).

Rainfall and rock cover were significant explanatory variables in species composition of all vertebrate taxa and of most invertebrate groups (Table 8). However, there was no concordance in the set of significant environmental associations of any vertebrate and invertebrate taxon (Table 8, 9). Rainfall, elevation, and rock cover were significantly associated with both total vertebrates and total invertebrates (Table 8), but explained only 22.7% and 13.3% of deviance, respectively (Appendix S1: Table S2).

DISCUSSION

Our study is one of the most comprehensive regional analyses of the congruence of vertebrate and invertebrate diversity and distribution. We considered invertebrate taxa at the level of family

rather than order to avoid the potential masking of important patterns through the lumping of ecologically diverse groups, we obtained a mechanistic understanding of cross-taxon congruence patterns of richness and composition, and we examined the role of sampling intensity as a factor influencing congruence patterns. We found poor congruence in richness and composition among vertebrates and invertebrates, along with marked variation in their environmental associations, and showed that poor congruence was not simply an artifact of low sampling intensity.

Species richness and composition of the four vertebrate classes were at best only weakly positively associated with that of invertebrates, and even then, just with a subset of families. These findings add to growing evidence that geographic patterns of vertebrate diversity and distribution are often poorly correlated with those of invertebrates in tropical ecosystems (Kremen 1992, Lawton et al. 1998, Bennett et al. 2009, de

Table 6. Environmental associations of invertebrate and vertebrate species richness, showing strength of relationship of log cover, rock type, rainfall, elevation, and fire covariates (remaining environmental covariates shown in Tables 5 and 7).

Taxon	No. of logs	Rainfall (mm)	Elevation (m)	Fire severity			Fire frequency			Rock type		
				0	1	2	Recent	Intermittent	long unburnt	Laterite	Other	Sandstone
Invertebrates												
Carabidae			-0.006*								-0.64*	0.71**
Chloropidae												
Curculionidae												
Formicidae		-0.002***									0.13**	-0.06
Lycosidae								1.83**		1.73*		
Phoridae		-0.004**										
Ptinidae		-0.01**										
Salticidae		0.001*										
Scarabaeidae												
Staphylinidae		0.002*										
Tenebrionidae		-0.008***										
Zodariidae		0.003*										
Vertebrates												
Amphibians			-0.004**								-0.38	0.001*
Birds	0.003	-0.001***										
Mammals											-0.25	-0.98*
Reptiles								0.26**		0.03		
Total												
Invertebrates		-0.002***										
Vertebrates		-0.0006**	-0.0008*									
Species		-0.0009***										

Notes: Positive associations are indicated in bold and negative associations in italics. For GLM model statistics, see Appendix S1: Table S2, and for description of environmental variables, see Appendix S1: Table S1. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Andrade et al. 2014), as has been shown in other climatic zones (Wilcox et al. 1986, Prendergast et al. 1993, Oliver et al. 1998, French 1999, Lund and Rahbek 2002). Some studies have even reported inverse richness patterns of vertebrate and invertebrate taxa (Oliver et al. 1998, Vessby et al. 2002), and we found examples of this involving amphibians, reptiles, and mammals.

Our results indicate that, of the different vertebrate groups, patterns of diversity and distribution of birds were most congruent with those of invertebrate taxa. We found positive associations between birds and eleven of our twelve invertebrate families in either species richness or composition. This suggests that when compared to invertebrates, birds respond more similarly to environmental gradients than do other vertebrate groups (Ricketts et al. 2002, Lovell et al. 2007, Duan et al. 2016), although their similarly high dispersal abilities associated with flight

might also be a contributing factor. However, despite birds showing higher and more consistent spatial congruence with invertebrates than did other vertebrate groups, the level of congruence was still low. The predictive power of birds in our study was always <30%, and such consistently weak relationships mean that there is little value in their application as umbrellas for invertebrates. These findings concur with the vast majority of bird-invertebrate congruence studies, which consistently show birds to be poor surrogates for ground-dwelling invertebrates (Burbidge et al. 1992, Lawton et al. 1998, Vessby et al. 2002, de Andrade et al. 2014). This is the case even if relationships are statistically significant; for example, a cross-taxon congruence study in southeastern Australia found that birds were significantly correlated with native bees, whereas reptile diversity was not, but the variation explained was only 9.5% and 4.5% for species

Table 7. Environmental associations of invertebrate and vertebrate species richness, showing strength of relationship of soil covariates (remaining environmental covariates shown in Tables 5, 6).

Taxon	Soil texture			Soil depth			Soil color			
	Clay	Loam	Sand	0–10 cm	10–40 cm	>40 cm	Brown	Gray	Pale	Yellow-red
Invertebrates										
Carabidae										
Chloropidae										
Curculionidae		0.31	<i>-0.39*</i>							
Formicidae										
Lycosidae							<i>-0.76*</i>	<i>-0.44</i>	1.04**	
Phoridae										
Ptinidae										
Salticidae					0.07	<i>-0.26</i>				
Scarabaeidae										
Staphylinidae										
Tenebrionidae										
Zodariidae		0.42	<i>-0.59*</i>				<i>-0.27</i>	<i>-0.27</i>	<i>-0.16</i>	
Vertebrates										
Amphibians										
Birds										
Mammals		<i>-0.46</i>	0.39*							
Reptiles										
Total										
Invertebrates										
Vertebrates										
Species										

Notes: Positive associations are indicated in bold and negative associations in *italics*. For GLM model statistics, see Appendix S1: Table S2, and for description of environmental variables, see Appendix S1: Table S1.

* $P < 0.05$; ** $P < 0.01$.

richness and composition, respectively (Yong et al. 2018). Birds are also typically poor surrogates for non-epigeic taxa (Lawton et al. 1998, French 1999, Lund and Rahbek 2002, Vessby et al. 2002, Williams et al. 2006, Ekroos et al. 2013, Foord et al. 2013, Eglington et al. 2015).

Combining vertebrate taxa did not improve congruence with invertebrates in terms of species richness but did improve congruence in species composition. Poor congruence in richness was because different vertebrate taxa often showed inverse relationships to each other, meaning these relationships were canceled out when vertebrate taxa were combined. Combining vertebrate groups into a single measure can therefore mask relationships of its component taxa, and so particular vertebrate taxa are more likely to act as umbrellas for invertebrate richness when used in isolation. In contrast, there were no negative correlations involving species composition, and so there was no canceling out of relationships when all vertebrate groups were combined.

These findings indicate that factors driving variation in species composition are very different from those driving variation in species richness. Hence, taxa that might act as a useful umbrella in relation to richness will not necessarily do so for composition. Su et al. (2004) found similar inconsistencies in bird–butterfly congruence across a large montane landscape, as birds were useful in representing butterfly composition but not richness. Ideally, a useful umbrella taxon should be representative in terms of both species richness and composition, as instances of congruence across multiple measures of biodiversity provide the most compelling tool for effective conservation planning (Gioria et al. 2011).

It is possible that low congruence in geographic patterns of different faunal taxa is at least partly an artifact of low sampling intensity, given that surveys typically fail to detect many animal species that are present. We found that sampling intensity did indeed affect congruence results, with data from multiple surveys compared

Table 8. Environmental associations of invertebrate and vertebrate species composition, showing the best combination of explanatory environmental covariates: vegetative and ground cover, rainfall, and elevation (remaining environmental covariates shown in Table 9).

Taxon	Percent cover								No. of logs	Rainfall (mm)	Elevation (m)
	Bare ground	Rock	Litter	Hummock grass	Perennial grass	Annual grass	Sedge	Other ground Canopy			
Invertebrates											
Carabidae		4.8**					3.1**				
Chloropidae			2.2			5.2**				2.4	
Curculionidae										3.1**	
Formicidae		2.7***								7.9***	2.8***
Lycosidae			3.1*			2.9*		2.7*	2.2		
Phoridae		2.5								14.9***	
Ptinidae										5.9**	
Salticidae		5.1***						2.3*	2.3*	9.3***	
Scarabaeidae	3.9***							2.5*		2.7**	
Staphylinidae		4.5**								3.2**	
Tenebrionidae								4.2**		11.7***	
Zodariidae									2.6	3.1*	
Vertebrates											
Amphibians		3.4**								14.3***	3.5**
Birds	2.6**	3.6***								10.3***	2.5**
Mammals		4.6**								7.1***	
Reptiles		7.5***						2.9***		6.5**	3.3***
Total											
Invertebrates		2.9***								7.8***	2.6***
Vertebrates		4.8***								10.4***	2.6***
Species		3.7***								9.5***	2.7***

Notes: Data denote the percent contribution of each covariate to species composition. Significance levels determined using non-parametric Mantel test with 999 permutations: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For DistLM model statistics, see Appendix S1: Table S2, and for description of environmental variables, see Appendix S1: Table S1.

with a single survey increasing the number of significant correlations for most vertebrate groups. However, for most pairs of vertebrate–invertebrate groups there were no or negligible improvements in correlation. This included correlations involving mammals, which were substantially improved by data from multiple surveys for only one of the 12 invertebrate families (ants). Such a marginal improvement occurred despite mammals having especially low detectability—the single 2014–2015 survey detected only 40% of the total mammal species recorded when pooling across three survey sessions. Mammal detectability is notoriously low in faunal surveys more generally (Einoder et al. 2018) but is likely to be especially low in our study due to precipitous declines in mammal populations that have occurred across northern Australia over recent decades (Woinarski et al. 2010, 2011). The limited role of detectability in explaining our findings of low congruence is also illustrated by results for amphibians, for which the single-survey data

showed somewhat better congruence with invertebrate taxa than did the multiple-survey data, even though it detected fewer species.

We acknowledge that even our multi-year sampling data are likely to be under-representative of the total vertebrate communities that occur at our study sites. We also acknowledge that the detectability of most of our invertebrate species is likely to be low. Species detectability of invertebrates is rarely quantified in invertebrate surveys (Kellner and Swihart 2014), but it is often low even after repeat sampling (Kery and Platner 2007, Driscoll 2010, Hudgins et al. 2012). However, given that increased sampling intensity of vertebrates led to only marginal improvements in congruence, we would expect similarly marginal improvements with increased sampling intensity for invertebrates. The extent to which detectability biases may confound congruence patterns requires further investigation, but it seems highly unlikely that further sampling of either vertebrates or invertebrates would improve

Table 9. Environmental associations of invertebrate and vertebrate species composition, showing the best combination of explanatory environmental covariates: fire, rock type, and soil (remaining environmental covariates shown in Table 8).

Taxon	Fire severity	Fire frequency	Rock type			Soil texture			Soil depth (cm)	Soil color			
			Laterite	Other	Sandstone	Clay	Loam	Sand		Brown	Gray	Pale	Yellow-red
Invertebrates													
Carabidae					2.8*						3.8**		
Chloropidae		3.3*			8.7***								
Curculionidae			8.3***	4.9***	5.1***				2.4*				
Formicidae			2.4**										
Lycosidae		2.8*		7.6**		2.9*					2.5		
Phoridae				5.6**							2.5		
Ptinidae												2.6	
Salticidae											2.8*		
Scarabaeidae													
Staphylinidae				2.4**							3.3*		
Tenebrionidae								4.3**					
Zodariidae					2.7*		2.9*	2.7*			4.2**		
Vertebrates													
Amphibians			2.6*										
Birds													
Mammals						2.5*							
Reptiles		2.2*	3.3**									2.1*	
Total													
Invertebrates													
Vertebrates													
Species													

Notes: Data denote the percent contribution of each covariate to species composition. Significance levels determined using non-parametric Mantel test with 999 permutations: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For DistLM model statistics, see Appendix S1: Table S2, and for description of environmental variables, see Appendix S1: Table S1.

congruence in our study system substantially enough to reach the 60–80% threshold required for effective prediction (Fleishman et al. 2005, Lovell et al. 2007, Leal et al. 2010).

The assessment that poor congruence is not just a sampling artifact is supported by our analyses of environmental associations. Poor congruence in geographic patterns of vertebrates and invertebrates can be expected if they show differing responses to environmental variables (Nelson and Nelson 2001, Ricketts et al. 2002, Heino et al. 2005, 2009). Our finding of very different environmental associations of vertebrates and invertebrates, for both richness and composition, concurs with the low congruence results. Environmental associations varied widely among both vertebrate and invertebrate taxa, and they were especially idiosyncratic among invertebrates. The more specialized habitat requirements and complex life histories of many invertebrates likely contribute to their variable environmental associations and therefore to the

poor performance of vertebrates as umbrellas for invertebrate diversity (Mac Nally et al. 2002, Viterbi et al. 2013). The different environmental associations of vertebrates and invertebrates imply that their local conservation needs and management priorities are very weakly aligned.

We note that our findings of low cross-taxon congruence apply to the 0.25-ha scale at which we sampled, which is typical for biodiversity survey in Australia (Woinarski et al. 2002, Kutt and Woinarski 2007, Eyre 2012) and elsewhere in the world (Brown and Heske 1990, Tietje et al. 1991, Hanya 2005, Sreekar et al. 2018). Cross-taxon congruence might be expected to be higher if assessed at larger spatial scales (Dumbrell et al. 2008, Westgate et al. 2014, 2017), especially if such scales over-ride the finer-scale patterning typically shown by invertebrates (Ferrier et al. 1999, French 1999, Pik et al. 2002). This is a fruitful area for future research.

In conclusion, our study has shown that geographic patterns of vertebrate richness and

composition are weakly correlated with those of terrestrial invertebrates and do not come close to providing the predictive power required for them to be effective umbrellas for invertebrates in conservation planning. We have also shown that poor congruence is highly unlikely to be just an artifact of inadequate sampling intensity. Our findings add to the growing body of evidence that the use of well-studied, charismatic taxa as surrogates of highly diverse understudied groups is not an effective solution to protecting all biodiversity (Panzer and Schwartz 1998, Andelman and Fagan 2000, Ozaki et al. 2006, Santi et al. 2010, Dorey et al. 2018). Effective planning for the conservation of invertebrates requires direct empirical data on their diversity and distribution patterns.

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