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Introduced cats eating a continental fauna: invertebrate consumption by feral cats *Felis catus* in Australia

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Key words: insects; arthropods; diet; invasive predator; predation.

Abstract

Context

Recent global concern over invertebrate declines has drawn attention to the causes and consequences of this loss of biodiversity. Feral cats *Felis catus* pose a major threat to many vertebrate species in Australia, but their effect on invertebrates has not previously been assessed.

Aims

The objectives of our study are to: (1) assess the frequency of occurrence (FOO) of invertebrates in feral cat diets across Australia and the environmental and geographic factors associated with this variation; (2) estimate the number of invertebrates consumed by feral cats annually and the spatial variation of this consumption; and (3) interpret the conservation implications of these results.

Methods

From 87 Australian cat diet studies, we modelled the factors associated with variation in invertebrate FOO in feral cat diet samples. We used these modelled relationships to predict the number of invertebrates consumed by feral cats in largely natural and highly modified environments.

Key results

In largely natural environments, the mean invertebrate FOO in feral cat dietary samples was 39% (95% CI: 31%-43.5%), with Orthoptera the most frequently recorded Order, at 30.3% (95% CI: 21.2% - 38.3%). The highest invertebrate FOO occurred in lower rainfall areas with lower mean annual temperature, and in areas of greater tree cover. Mean annual invertebrate consumption by feral cats in largely natural environments was estimated to be 769 million individuals (95% CI: 422-1,763 million) and in modified environments (with mean FOO of 27.8%) 317 million invertebrates year^{-1}, giving a total estimate of 1,086 million invertebrates year^{-1} consumed by feral cats across the continent.

Conclusions

The number of invertebrates consumed by feral cats in Australia is greater than estimates for vertebrate taxa, although the biomass (and hence importance for cat diet) of invertebrates taken would be appreciably less. The impact of predation by cats on invertebrates is difficult to assess due to the lack of invertebrate population and distribution estimates, but cats may pose a threat to some large-bodied narrowly restricted invertebrate species.

Implications

Further empirical studies of local and continental invertebrate diversity, distribution and population trends are required to adequately contextualise the conservation threat posed by feral cats to invertebrates across Australia.

Short summary

Insect decline across the globe calls for urgent attention to conservation impacts from potential threats. Feral cats consume substantial numbers of Australian birds, reptiles and mammals, but their consumption of invertebrates and potential impacts on this group have not previously been estimated. We found that feral cats consume more than 1 billion invertebrates per year in Australia, with highest take in arid/semi-arid areas. The number of invertebrates eaten by cats is greater than the number of mammals eaten, but being much smaller in body size, invertebrates contribute a substantially smaller proportion of dietary biomass. The impacts of feral cats on invertebrates are difficult to assess, due to the lack of abundance and distribution estimates for invertebrates across Australia.

Introduction

Invertebrates are the most numerous and diverse of all terrestrial and freshwater macrobiota on Earth and thus contribute considerably to global biodiversity (Wilson 1987). Recent research has demonstrated a global pattern of insect loss, with associated consequences for ecosystem function, productivity and services (Fonseca 2009; Dirzo *et al.* 2014; Thomas 2016; Hallmann *et al.* 2017; Vogel 2017; Lister and Garcia 2018; Eisenhauer *et al.* 2019; Sánchez-Bayo and Wyckhuys 2019). Key threats to invertebrates include anthropogenic disturbance, such as habitat degradation and loss, climate change, invasive species, and broad-scale use of pesticides (Benton *et al.* 2002; Potts *et al.* 2010; Thomas 2016; Sánchez-Bayo and Wyckhuys 2019). While invasive species are not recognised as the primary driver of insect declines generally, some are responsible for profound ecological impacts on invertebrate communities at both local and landscape scales, and on individual invertebrate species. For example, invasive plants have negatively impacted many local invertebrate communities around the globe (van Hengstum *et al.* 2014), invasive rodents have had devastating effects on many island invertebrates (St Clair 2011), and introduced species (i.e., rats, goats, pigs, chameleons, snails, ants, flatworms, and plants) have caused the extinction of hundreds of species within the Hawaiian land snail family Amastridae (Régnier *et al*. 2015).

Australia is recognised globally for its diverse, endemic biota. With continental island-like biogeography, introduced fauna has had devastating effects. Two invasive vertebrate predators, the European red fox *Vulpes vulpes* and the domestic cat *Felis catus*, have been implicated in the decline and extinction of many vertebrate species, particularly mammals (Woinarski *et al.* 2015). There are an estimated 3.77 million pet cats in Australia (Animal Medicines Australia 2019), 0.7 million feral cats in highly modified environments ('stray' cats), and between 1.4 and 5.6 million feral cats across Australia's natural environments (with this number varying in response to rainfall conditions) (Legge *et al*. 2017). In recent reviews collating more than 100 cat diet studies across the continent, the magnitude of consumption by cats was assessed for birds, reptiles and mammals in Australia (Woinarski *et al.* 2017a; Woinarski *et al.* 2018; Murphy *et al.* 2019). Cats in Australia consume more than 2 billion individuals from these vertebrate groups each year, with records of consumption compiled for at least 59% of extant native mammals (170 species), 46% of birds (338 species) and 26% of reptiles (258 species), including many threatened species (Woinarski *et al.* 2017b; Woinarski *et al.* 2018; Woolley *et al.* 2019). This possibly takes a substantial toll on Australian wildlife.

Australia's invertebrates are poorly studied compared with its vertebrates, as is generally the case around the world. Currently, most Australian invertebrate species remain undescribed and, of those that are described, the overwhelming majority lack an assessment of population trends and spatial distribution (Braby 2019). Ten known invertebrate extinctions have occurred in Australia since European settlement in 1788, and while there are many anecdotal indications of decline for many additional invertebrate species, the limited extent of monitoring and limited knowledge of threats renders it difficult to obtain definitive evidence for any overall change (Rix *et al*. 2017; Braby 2019; Watts *et al.* 2019). Therefore, while there may be a decline in Australian invertebrate biodiversity, there is little evidence of the direct causes of this potential decline overall or across individual species. Sands (2018) highlighted the importance of habitat loss and disturbance, climate change, and inadequate conservation policy and protected area legislation for Australian insect conservation. Habitat loss was the most common threatening process that drove, or likely drove, the ten known invertebrate extinctions in Australia, and four of the ten species were affected by invasives, e.g., introduced house mice *Mus musculus* were implicated in the extinction of Lord Howe ground weevil *Hybomorphus melanosomus*, introduced weeds and snails were implicated in the extinction of Geraldton land snail *Bothriembryon whitleyi*, and introduced snails and slugs were implicated in the extinction of Helicarionid land snail *Helicarion castanea* and the Albany carnivorous snail *Occirhenea georgiana* (Braby 2019).

Although considered a key threat to many vertebrate species, the potential impact of predation by cats on invertebrates across Australia has not previously been considered. This focus on assessment of the impacts of cat predation on vertebrate conservation, but not on invertebrate conservation, is almost pervasive in cat dietary studies, and in response Eisenhauer (2018) urged complementary consideration of the incidence and impacts of cat predation on invertebrate species: our assessment here is stimulated in part by this call.

Feral cats now occupy the entire continent of Australia and many off-shore islands (Abbott 2008; Legge *et al.* 2017) and the magnitude of the take of invertebrate prey by this invasive predator may be of conservation significance. In a previous review of feral cat diet across Australia, Doherty *et al.* (2015) found that feral cats consumed invertebrates most frequently of all the prey groups considered, with greatest invertebrate consumption associated with harsher environmental conditions, i.e. lower rainfall and productivity. Here we use a larger set of sources to revisit that review, but focus our attention on invertebrates rather than all taxonomic groups. We therefore aim to: (1) assess the frequency of occurrence of invertebrates (in total and the frequency for main invertebrate groups) in feral cat diet across Australia and the environmental and geographic factors associated with this variation; (2) estimate the number of invertebrates (in total and numbers for main invertebrate groups) consumed by feral cats annually and the spatial variation of this consumption; and (3) interpret the potential conservation implications of these results. We present estimates of the number of invertebrates consumed by feral cats in both largely natural and highly modified environments, but do not present such an estimate for pet cats because no relevant studies have reported the quantities of invertebrates consumed by these animals.

Methods

Our analysis follows Woinarski *et al.* (2017a), Woinarski *et al.* (2018) and Murphy *et al.* (2019) where, respectively, the numbers of birds, reptiles and mammals killed by cats in Australia were assessed.

Collation of studies

We collated data from 87 dietary studies (58 published and 29 unpublished, Table S1) across Australia that quantitatively assessed the frequency of occurrence (FOO) of invertebrates in feral cat scat or stomach samples (Fig. 1). Because some studies reported data for separate sub-sites or conditions at the same study location, our observations (102) exceed the number of studies assessed (87) and comprise a total of 10,241 scat and stomach samples of feral cat diet (Table S1).

Although in at least some Australian environments invertebrate abundance may vary markedly among seasons, and the occurrence of invertebrates in the diets of predatory mammals may correspondingly show marked seasonal variation (Green and Osborne 1981), we do not consider seasonal variation in feral cat diet, because many of the studies collated here spanned several seasons, and/or the time of year covered by the sampling was not specified. Furthermore, we do not include year because a consistent directional trend in diet over decadal scales is implausible (studies were conducted between 1969 and 2019).

Most studies did not report invertebrate taxa to species level, therefore we grouped occurrence records into the following broad invertebrate categories: ants (Formicidae) and termites (Isoptera); beetles (Coleoptera); butterflies and moths, including caterpillars (Lepidoptera); centipedes (Chilopoda); cicadas and other Hemiptera (Hemiptera); cockroaches (Blattodea), crickets and grasshoppers (Orthoptera); crustaceans (Crustacea); dragonflies (Odonata); flies, but excluding maggots (Diptera); mantids (Mantodea); phasmids (Phasmatodea); scorpions (Scorpionida); spiders (Araneae); wasps (Aculeata); and ‘other’ or ‘unidentified’.

We recognise that there are many potential sources of bias in the examination of cat stomach or scat samples for invertebrates. A bias toward under-reporting of invertebrate taxa is likely where those taxa are soft-bodied or easily digestible and leave little or no trace within a stomach or scat, e.g., spiders, molluscs, caterpillars. The number of invertebrates in a scat sample is also more likely to be underestimated if many of the same invertebrates were ingested together and if the invertebrate species was small-bodied (Dickman and Huang 1988). Furthermore, the occurrence of some invertebrates in cat dietary samples may arise from incidental consumption (e.g., of maggots within carrion) rather than deliberate take by cats of invertebrate prey.

The quality of invertebrate assessments may also be affected by observer effort and high variability among studies, such as variations in observer commitment to search for tiny fragments of invertebrate remains in each sample. High effort studies may therefore report higher invertebrate frequencies in cat diet. We suspect that many of the studies we assembled had primary interest in the detection of vertebrates (especially threatened mammal species) in cat dietary samples, and may have been less diligent in comprehensive recording of collateral invertebrate presence. We assume accurate identification of invertebrate groups, but acknowledge that this would vary depending on observer experience and the difficulty associated with identification of invertebrate body fragments. Overall, due to a large bias toward under-reporting in the studies we collated, we consider the estimates we derive to be conservative.

Variation in frequency of occurrence of invertebrates in feral cat diet

Environmental and geographic factors potentially associated with variation in FOO of invertebrates (and invertebrate groups) across Australia were evaluated using generalised linear models (GLMs) with a binomial error structure and logit link, which is appropriate for proportion (frequency) data and weighted according to study sample size. All statistical analyses were run using the statistical software R (ver. 3.6.1; R Core Team 2019). From the location of each study, we determined mean annual temperature (Australian Bureau of Meteorology 2019a), mean annual rainfall (Australian Bureau of Meteorology 2019b), mean tree cover within a 5km radius (Hansen *et al.* 2003) and topographic ruggedness (standard deviation of elevation within a 5km radius) (Jarvis *et al.* 2008). We derived a composite variable to express whether a study was located on an island or the mainlands of Australia or Tasmania, combined with the size of the island (in km^2), as per Woinarski *et al.* (2017a), Woinarski *et al.* (2018) and Murphy *et al.* (2019):

$$island\ size\ index = log10\ (minimum\ \left\{1, \frac{area}{10000}\right\}),$$

where *area* is island area in km^2. The Australian and Tasmanian mainlands (area ≥10,000 km^2) have an index of 0, while islands <10,000 km^2 (which encompasses all Australian islands smaller than Tasmania) have negative values, which became increasingly negative with decreasing island area. We also scored a factor to indicate whether or not a study occurred in a modified environment (i.e., rubbish dumps, semi-urban areas) and included this factor in all models to control for modified environments. To allow non-linear trends, all variables were included as quadratic or polynomial terms in GLMs.

We used a model-averaging approach to evaluate relative variable importance from a set of models representing all variable combinations, as well as an interaction term between rainfall and temperature (R package MuMIn: Barton 2019). Each model was weighted according to Akaike weight (w_i), equivalent to the probability of a particular model being the best in the candidate set, and based on a second order form of Akaike Information Criteria for small sample size, $QAIC_c$, used instead of AIC_c when models are overdispersed (Burnham and Anderson 2003). Full model-averaged coefficients were derived from a 95% confidence model set (i.e., cumulative $w_i = 0.95$) to predict invertebrate FOO in feral cat diet across Australia.

Number of invertebrates consumed by feral cats in largely natural environments

Most of the collated studies reported frequency rather than the number of individual invertebrates in each sample. However, in 20 studies (Table S2), tallies were given for the number of individual invertebrates in those samples that contained invertebrates. Exploratory analysis indicated no significant difference between invertebrate FOO derived from scat and stomach samples. However, it is often difficult to accurately account for (count) individual invertebrates from remnants of body parts or chitinous exoskeletal remains in scats whereas whole invertebrate individuals may be present in stomach contents (Dickman and Huang 1988). Therefore, we used only studies of stomach samples (n=16, Table S2) to examine the relationship between the number of individuals per sample and the frequency of occurrence of invertebrates in diet studies. Invertebrate counts in these studies were based upon the number of whole individuals, as well as identifiable body parts that could be attributed to a single individual, e.g. two wings. We modelled the relationship between the number of individual invertebrates per sample and the FOO of invertebrates in each dietary study using a linear least-squares regression model. This model was used to predict the mean number of individual invertebrates per dietary sample that contained invertebrates. Note that these tallies assume that all invertebrate individuals consumed by a cat are not so digested as to be unrecognisably distinct: it is plausible, and indeed quite likely, that observers may have under-counted the actual number of invertebrates within examined cat stomachs.

The number of invertebrates consumed by feral cats km^{-2} day^{-1} was calculated as the product of: (1) feral cat density projected across Australia, based on about 100 local estimates of cat densities (Legge *et al.* 2017); (2) modelled invertebrate FOO in feral cat diet samples across Australia; and (3) the predicted number of individual invertebrates in samples that contained invertebrates. As a caveat, we note that one recent study (Rees *et al*. 2019), in a dense temperate forest, concluded that local cat density was appreciably higher than the national modelling of Legge *et al*. (2017) predicted, perhaps in part reflecting the sparse data base from this environment available to Legge *et al*. (2017). The three chains of analysis described above provided a spatial representation of the number of invertebrates consumed by feral cats per day, and when multiplied by 365.25 (days in a year) provided a spatial representation of the number of invertebrates consumed by feral cats km^{-2} $year^{-1}$. We estimated uncertainty by simultaneously bootstrapping (20,000 times) the three underlying datasets (1–3 above) following the approach used by Loss *et al*. (2013). For each random selection of these underlying data, we recalculated the total number of invertebrates consumed and report the 2.5% and 97.5% quantiles for these 20,000 values.

Number of invertebrates consumed by feral cats in highly modified landscapes

Only seven studies were conducted in highly modified environments, including peri-urban areas and rubbish dumps (Table S1). This small sample size did not allow for reliable assessment of spatial variability as for feral cats in natural environments; therefore we used mean invertebrate FOO across these seven studies, multiplied by the expected number of individuals in cat samples with that frequency, and then multiplied by the density (and hence population size) of feral cats in these environments, as estimated by Legge *et al.* (2017). We compared this calculated estimate with that obtained from feral cat studies in largely natural environments using a Mann-Whitney *U*-test, but note that the small sample size from highly modified environments constrains the reliability of such comparisons.

Comparison of frequency of invertebrates in feral cat diet with that of other co-occurring mammalian predators

Studies from our collation that included comparative sampling of co-occurring feral cat, fox and dingo (including wild dog) *Canis familiaris/dingo* diets (n=27, Table S3) were used to compare invertebrate FOO between co-occurring predators using Wilcoxon matched-pairs tests.

Results

Feral cats in largely natural environments

Based on 87 reports from largely natural environments in Australia, the mean FOO of invertebrates in feral cat diet was 39% (95% CI: 31–43.5%), but ranged across studies from 0 to 100% (Table S1). Highly influential variables predicting invertebrate FOO in feral cat diet across Australia were mean annual rainfall (interacting with mean annual temperature), and tree cover (Table 4, Fig. 2), with FOO not significantly different in island and continental samples. A higher frequency of invertebrates occurred in feral cat diet in lower rainfall areas with lower mean annual temperature (Fig. 2a). Invertebrate FOO did not vary with rainfall when the mean annual temperature was above 26°C (Fig. 2a). Invertebrate FOO increased with tree cover, but peaked at intermediate tree cover (40 – 60%) (Fig. 2b). These modelled relationships were used to project the frequency of occurrence of invertebrates in feral cat diets across Australia (Fig. 3a).

The number of individual invertebrates present in cat scats or stomachs was significantly positively correlated with invertebrate FOO (Fig. 4). Thus, a study reporting a high frequency of invertebrates in the samples analysed was also likely to report that each of those samples with invertebrates included many individual invertebrates.

From these FOO values, the numbers of invertebrates in cat samples, and the numbers of feral cats, we calculated that, in an average year, the number of invertebrates consumed by feral cats across largely natural environments in Australia is 769 million (95% CI: 422–1,763 million), i.e. 101 invertebrates km^{-2} $year^{-1}$ (Fig. 3b). Thus, feral cats in largely natural environments consume about 2.1 million invertebrates day^{-1}, with an average individual feral cat eating about 371 invertebrates $year^{-1}$.

Feral cats were reported to consume invertebrates from many taxonomic groupings, but very few studies reported identifications to species level (Table S2). From dietary studies that categorised invertebrates by taxonomic group, Orthoptera (crickets and grasshoppers, 30.3% [95% CI: 21.2–38.3]), Chilopoda (centipedes, 7.9% [4.4–10.6]), Coleoptera (beetles, 7.3% [5.2–12.2]), Arachnida (spiders, 4.9% [2.3–6.5], scorpions, 1.6% [0.8–2.2]) and Lepidoptera (butterflies and moths, 1.9% [1.0–5.1]) occurred most frequently in cat diets. There was substantial variation among studies depending largely on the highly influential variables rainfall, tree cover and topographic ruggedness. A decrease in Orthoptera and Chilopoda FOO was observed with increasing ruggedness and tree cover respectively (Fig. 5a, b). An increase in Coleoptera FOO was observed in areas of low rainfall, and in areas with intermediate (20–30%) and greatest (≥ 60%) tree cover (Fig. 5c, d).

The total number of individual invertebrates consumed per year was highest for Orthoptera (472 million $year^{-1}$ [95% CI: 221–1,061 million]), Coleoptera (65 million $year^{-1}$ [40–434 million]), Chilopoda (64 million $year^{-1}$ [32–151 million]), Arachnida (spiders, 39 million $year^{-1}$ [17–115 million], scorpions, 13 million $year^{-1}$ [7–34 million]) and Lepidoptera (14 million $year^{-1}$ [8–158 million]).

Feral cats in highly modified environments

On the basis of seven studies conducted in highly modified environments in Australia (Table S1), 317.3 million invertebrates $year^{-1}$ were estimated to be consumed by feral cats (where the mean invertebrate FOO across the seven studies [27.8%] was multiplied by the expected number of individuals in samples with that frequency of invertebrates [4.34, Fig. 4], the number of days in a year [365.25], and by total feral cat population size in modified environments [0.72 million, Legge *et al.* 2017]). Combined with estimates of consumption by feral cats in largely natural environments, this gives a total estimate of 1,086 million invertebrates $year^{-1}$ consumed by feral cats across the continent.

The mean invertebrate FOO in feral cat diet from seven studies in modified habitats (28%) was not significantly different from the mean estimate of invertebrate FOO in largely natural environments (mean 39%; Mann-Whitney *U*-test, $z = 0.11$, $P = 0.45$).

Comparison of frequency of invertebrates in feral cat diet with that of other co-occurring mammalian predators

From 14 studies reporting the dietary composition of co-occurring cats and dingos (Table S3), invertebrate FOO was significantly lower in dingo diet (mean ± SE, 11.5 ± 2.6%) than cat diet (32.6 ± 6.4%) (Wilcoxon matched-pairs test, $z = 0.79$, $P = 0.003$). From 18 studies of co-occurring cat and fox diet (Table S3), invertebrate FOO was significantly higher in fox than cat diet (47.7 ± 5.9% and 34.6 ± 4.4% respectively) ($z = 0.70$, $P = 0.003$).

Discussion

The number of invertebrates consumed by feral cats annually in Australia is greater than the number of mammals consumed, the feral cat's dominant prey group (i.e., 1.1 billion invertebrates [95% CI: 422–1,763 million] *vs*. 815 million mammals [530–1,414 million]). In terms of comparative biomass, however, substantially smaller body size of invertebrates than mammals results in invertebrates contributing far less to total feral cat dietary biomass than mammals. Most of our collated studies reported that invertebrates were found frequently in feral cat diet but contributed a much smaller proportion of dietary biomass per sample.

Mammals occur much more frequently than invertebrates in the diet of feral cats across the continent (mean frequency of occurrence: 70%, Murphy *et al.* 2019), with invertebrate FOO (39%, current study; 36% Doherty *et al*. 2015) being similar to that of birds (32%, Woinarski *et al.* 2017a; 27% Doherty *et al*. 2015) and reptiles (26%, Woinarski *et al.* 2018; 24% Doherty *et al.* 2015). Although far less frequent than mammals, invertebrate individuals per dietary sample amount to triple (average of 4.3 individuals) that of mammals (average of 1.4 individuals) reported per dietary sample: i.e. individual cats consuming invertebrates may take several or many individuals per day. The average number of individual birds and reptiles consumed by cats per day is similar to that of mammals (1.3 and 1.9 individuals respectively, Woinarski *et al.* 2017a; Woinarski *et al.* 2018). Therefore, there is a comparatively lower yearly average of individual birds (272 million [169–508 million]) and reptiles (466 million [271–1,006 million]) consumed by cats compared with invertebrates (1.1 billion).

Our study collates much primary data, from about 100 local studies of cat density, and nearly 90 studies of the diet of feral cats (with collectively 10,675 cat dietary samples). It is a very substantial foundation, but we acknowledge caveats in the data and its interpretation, particularly in extrapolating to national scale estimates of total consumption by cats of invertebrates. For example, the primary studies of cat density and of cat diet collated here include only limited sampling of some environments, such as wet temperate forests (Rees *et al*. 2019). Furthermore, we cannot be certain that all of the researchers who reported on the contents of their cat dietary samples searched comprehensively for invertebrates: in some cases, their interest may have been more focused on the detection of threatened mammals in the diet of the cats they examined.

Nonetheless, there are no other continents with as many studies of feral cat density and diet (especially those that report consumption of invertebrates) as Australia. This adds robustness to our assessment, but makes inter-continental comparisons difficult. There have been many attempts to quantify the impacts of feral cats on the vertebrates of continental and island mainlands (Loss and Marra 2017) and other parts of the world (e.g., New Zealand: Gillies 2001; U.K.: Woods *et al*. 2003; Canada: Blancher 2013; U.S.A.: Loss *et al*. 2013; Japan: Shionosaki *et al*. 2015; Australia: Woinarski *et* *al*. 2017a, 2018; Murphy *et al*. 2019). Few (mostly focal) studies report invertebrate consumption (e.g., New Zealand: Gillies 2001; U.K.: Woods *et al*. 2003; Hungary: Biró *et al*. 2005; Brazil: Campos *et al.* 2007; Canary Islands: Medina and García 2007). It is difficult to extend comparisons from focal studies to continental reviews, as the frequency of invertebrate occurrence in the diet of feral cats can vary considerably between studies, e.g., 0.4% in Hungary (Biró *et al*. 2005), 69% in New Zealand (Gillies 2001), as it did among the component studies (from 0 to 100%) in our composite sample.

An analysis of multiple focal studies across the globe showed invertebrates are widely reported as important components of cat diet and comprise a large proportion of cat foraging activity budgets (Pearre and Maass 1998). Cat trophic niche breadth was found to be greater at low latitudes, primarily due to the frequent inclusion of invertebrates in these regions and during warmer seasons when invertebrates are most available (Pearre and Maass 1998). Many studies reporting high rates of predation by cats on invertebrates (e.g., Gillies 2001; Campos *et al.* 2007; Medina and García 2007) concede that this is likely because invertebrates are small-bodied and may be most abundant, while those reporting low or no predation (e.g., Woods *et al*. 2003; Biró *et al*. 2005) highlight considerable variability among individual cats and occasional feeding specialisation.

Bonnaud *et al.* (2010) reviewed feral cat diet on islands worldwide and reported that mammals (primarily rodents and rabbits) were the dominant prey of feral cats, while birds, reptiles and invertebrates were consumed less frequently. However, consumption of invertebrates generally tracked availability, with increased frequency in feral cat diet on tropical and subtropical islands (mean frequency ~35%), where invertebrates are assumed to occur in relatively higher abundance based on latitudinal gradients of species richness. Similarly, a recent study of feral cat diet across the New Caledonia archipelago found that feral cats preyed upon many of the endemic fauna of this biodiversity hotspot and consumed a diverse invertebrate prey ranging from small-bodied cicadas to large crustaceans, at an overall average dietary frequency of 35.2% (Palmas *et al*. 2017). Invertebrates were consumed most frequently in highly productive habitats on these islands during the wet season when invertebrate abundance increased. However, in low productivity habitats feral cats relied on invertebrates during the dry season when preferred prey was less abundant (Palmas *et al*. 2017). The perceived impact of feral cats on island wildlife has motivated several cat eradication efforts, and although invertebrates were typically not the primary taxa targeted for monitoring post-eradication, some positive benefits of mammalian predator (including feral cat) eradication to invertebrate populations on islands have been reported (e.g., Jones *et al*. 2016; Schori *et al.* 2018).

At a continental scale, the impact of feral cat consumption on total invertebrate abundance in Australia is difficult to assess, due to the lack of invertebrate population estimates (current and historical) and the many undescribed species present (Sands 2018; Braby 2019), and most importantly, the lack of controlled experiments addressing this issue. As a broad estimate, there are possibly around 320,000 invertebrate species in Australia, of which more than 70% are undescribed or undiscovered (Chapman 2009; Braby 2018). While it may be reasonable to assume that feral cat consumption may not amount to a substantial proportion of the (unknown) total number of individual invertebrates present at any one time across the continent, we acknowledge that we provide a conservative estimate of consumption due to a bias toward under-reporting of invertebrate taxa in cat dietary studies associated with the identification of tiny fragments of invertebrate body parts within scats or stomachs (Dickman and Huang 1988). This bias is confirmed by the high incidence of invertebrate (primarily Orthopteran and Hemipteran insect) consumption by cats in a study using cat-borne cameras (Hernandez *et al*. 2018). Concerns over targeted predation on particular taxonomic groups or species may well be pertinent.

With concern over global invertebrate declines, especially of larger-bodied insects of the order Orthoptera, Coleoptera and Lepidoptera (Dirzo *et al.* 2014), which were found here to be the favoured invertebrate prey groups of the feral cat in Australia, the impact of cat predation, either singly or in combination with other factors, on these invertebrate groups should not be dismissed. In our analysis, a high frequency of invertebrates in feral cat diets was associated with a correspondingly high number of individual invertebrates present in cat scats or stomachs sampled. Being opportunistic, a cat may take many invertebrates during any one predation event, and individual cats may specialise on particular prey types (Dickman and Newsome 2015), including some invertebrate species or groups. For example, among the studies we collated here, many found a high number of invertebrates in a single sample, for example 40 wingless grasshoppers *Phaulacridium vittatum* in a single cat stomach from Great Dog Island (Hayde 1992), 13 scorpions in a stomach from the Pilbara, WA (Martin *et al.* 1996), 54 Lepidoptera and four Odonata in one stomach in Fitzgerald River National Park, WA (O'Connell 2010), and an extraordinary 400 grasshoppers in one stomach from Witchelina Nature Reserve, SA (Woinarski *et al.* 2017c). This type of opportunistic predation may have a substantial impact if a cat focuses its search image and predation effort upon invertebrate taxa with a restricted or small population, such as short-range endemics. Many Australian species of subterranean invertebrates, gastropods, schizomids, myriapods, freshwater crustaceans, cicadas, centipedes, scorpions and mygalomorph spiders are considered short-range endemic invertebrates and are primarily limited by low fecundity, poor dispersal and a high degree of habitat specificity resulting in restricted distribution, rarity, and thus increased extinction risk (Harvey *et al*. 2011). Due to these characteristics, short-range endemics are highly threatened by habitat loss, habitat degradation and climate change (Harvey *et al*. 2011). Intense predatory pressure on short-range endemic invertebrates can have considerable detrimental impacts and compound extinction risk when acting synergistically with other key threats, e.g. predation on short-range endemic mygalomorph spiders in Perth, Australia, greatly exacerbated population decline due to habitat loss, invasive grasses and fire (Mason *et al*. 2018; Mason *et al*. 2019).

Of the 65 invertebrate species currently listed as threatened under the Australian Government's *Environment Protection and Biodiversity Conservation Act, 1999*, none have the feral cat listed as a threat, but commonly identified key threats include anthropogenically-induced factors such as habitat destruction and degradation due to urbanisation and agriculture, altered fire regimes, invasive species (mostly weeds), and climate change (Sands 2018; Taylor *et al.* 2018). Eastern Tasmania and many Australian islands have the greatest number of listed threatened invertebrates, with islands like Lord Howe and Norfolk Island particularly affected by anthropogenic disturbance and invasive species such as the black rat *Rattus rattus* (Priddel *et al.* 2003; Cresswell and Murphy 2016; Pickrell 2019). Although we did not find any variation in frequency of occurrence of invertebrates in cat diets on islands relative to the mainland, many Australian islands have up to threefold higher feral cat densities than the mainland (Legge *et al.* 2017; Taggart *et al*. 2019), with correspondingly higher overall predation pressure: this increased cat population density, and hence predation pressure, is magnified on smaller islands (Legge *et al.* 2017). Cat density on islands is often related to the seasonal abundance of seabirds and their breeding colonies, after which cats switch to other prey types, including invertebrates (Beh 1995). The synergistic effect of feral cat predation, particularly on range-restricted endemic island invertebrates, should be considered and evaluated.

In many cases, invertebrates officially listed as threatened are 'iconic' or 'charismatic' species, with a strong listing bias towards butterflies, spiders, molluscs, and beetles (Taylor *et al.* 2018), partly due to greater taxonomic knowledge of these groups, relatively higher public profile, or individual proponents advocating for their conservation (Cardoso *et al.* 2011; Braby 2018). Somewhat distinctive invertebrate groups (e.g., crickets, grasshoppers, centipedes, beetles, butterflies and moths, scorpions and spiders) were also those found here to be reported most frequently in feral cat diets, with preponderance of Orthoptera, Coleoptera and Lepidoptera among invertebrates in cat diet similarly reported in several studies globally (Eisenhauer 2018). Whether this is an accurate representation of predation by cats, or the result of greater ease of identification of these invertebrates is unknown. If accurate, this raises concern over an insufficiently recognised potential impact by feral cats on larger-bodied invertebrates (Eisenhauer 2018).

Of all the invertebrate taxonomic groups reported in feral cat dietary studies across Australia, Orthoptera (crickets and grasshoppers) were the most frequent (30.3%) and the most numerous (472 million individuals consumed year^{-1}) group in feral cat diet. Australia is home to an abundance of orthopteroid insects that generally occur across all terrestrial habitats (Rentz 1996), which is reflected in this invertebrate prey group being most commonly consumed by feral cats across the continent. Topographic ruggedness was the strongest predictor of the frequency of Orthoptera in feral cat diet, with a decline in frequency with increasing ruggedness. Most dietary studies conducted in topographically rugged areas were those associated with mountainous or escarpment areas, such as in Kosciusczko National Park, NSW (Watson, 2006), Barrington Tops National Park, NSW (Glen *et al*. 2011) and the Eastern Highlands, Vic (Jones and Coman 1981). Orthopteran populations are strongly regulated by climate, both directly through effects on life-history traits and indirectly through resource availability (Jonas *et al*. 2015; Yadav *et al*. 2018). Irruptive surges in Orthopteran abundance are commonly associated with seasonal temperature increases and snow-free months in mountainous alpine or sub-alpine environments (Green 2003) and feral cat consumption can track these surges. Overall, the invertebrate consumption rate by feral cats in these environments is severely limited by the restricted temporal window of invertebrate availability.

The most substantial consumption of invertebrates by feral cats in Australia occurred in arid and semi-arid areas, at similar frequency to that of reptiles in feral cat diets in these areas (aprox. 60%, Woinarski *et al.* 2018). Arid-dwelling mammals have shown the highest rates of decline and extinction over the last 200 years (Woinarski *et al.* 2015), and mammals occurring in low rainfall areas and falling within the 'critical weight range' (35–5500 g, Burbidge and McKenzie 1989) were found to have the greatest likelihood of being preyed upon by feral cats (Woolley *et al.* 2019). It is therefore likely that consumption of invertebrates and reptiles supports cat populations in arid areas, where mammals are now scarce, especially during dry periods between rainfall-driven booms (e.g., Paltridge *et al.* 1997). This pattern of highest dietary frequency of invertebrates and reptiles in feral cat diets in arid Australia was also reported in a previous continental-scale review of feral cat diet (Doherty *et al.* 2015), as well as many focal arid zone feral cat dietary studies (Catling 1988; Paltridge *et al.* 1997; Yip *et al.* 2015; Woinarski *et al.* 2017c; Read *et al.* 2019).

Australia's three main mammalian predators, the cat, European red fox and dingo, are flexible, opportunistic predators and are known to adjust their diet to varying degrees when preferred mammalian prey fluctuates and other prey groups become available or more abundant, for example during productivity pulses ('boom' or 'bust' periods) in arid regions (Paltridge 2002; Pavey *et al.* 2008; Yip *et al.* 2015; Spencer *et al.* 2017; Tatler *et al*. 2019). Invertebrate abundance has been shown to vary markedly with resource pulses in arid Australia, but dynamic taxon-specific responses buffer against the complete disappearance of invertebrates (Kwok *et al.* 2016; Gibb *et al*. 2019). Although most focal studies report low dietary overlap between feral cats and the dingo (Doherty 2015; Woinarski *et al.* 2017c), an analysis of dingo dietary records across Australia reported the highest frequencies of occurrence of invertebrates and reptiles in arid and semi-arid regions of Australia (Doherty *et al.* 2019). There is typically high dietary overlap between cats and foxes when analysed at a local scale, and high invertebrate predation has previously been reported in fox diets in local arid zone studies (e.g., Palmer 1995; Woinarski *et al.* 2017c). We found a slightly higher frequency of invertebrates in fox diets when compared with feral cat diets across a subset of our collated studies that assessed the diets of co-occurring mammalian predators, but a continental-scale review of fox diet is required to draw broad comparisons between cat and fox diet across the continent. The similarity in frequency of invertebrates in predator samples from low rainfall regions of Australia's interior is therefore likely to reflect prey availability rather than a difference in predator selectivity *per se*. For example, Mifsud and Woolley (2012) describe the emergence of centipedes from cracks in the ground following rainfall events in the arid/semi-arid Mitchell Grass Downs region, Qld, and an associated peak in centipede predation by feral cats and foxes during that time.

To fully appreciate the impact of the feral cat in Australia, we recognise the need for future conservation studies of Australian invertebrates (Braby 2018; Taylor *et al.* 2018; Braby 2019). Where possible, monitoring programs should endeavour to include invertebrate assessments, given that invertebrates are generally very diverse and highly endemic, they dominate the animal biodiversity of the continent, and they drive many important ecosystem processes (Cranston 2010; Rix *et al*. 2017; Andersen *et al.* 2018). Global concerns over invertebrate decline place a distinct focus on the need to address and estimate invertebrate conservation and biodiversity in Australia, including on the relative impacts of their putative threats (Braby 2019). Notably, although our estimates of invertebrate consumption by feral cats are conservative, the contribution of the feral cat to a decline in total invertebrate abundance in Australia is unlikely. However, targeted cat predation on populations of short-range endemic invertebrate species may threaten some of these species and contribute substantially to localised decline and changes in community composition.

Conflicts of interest

The authors declare no conflicts of interest.

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Supplementary material

Supplementary Table S1 provides a list of published and unpublished studies reporting the frequency of occurrence of invertebrates in the diet of feral cats in Australia and the environmental and geographic factors associated with each study site.

Supplementary Table S2 provides the frequency of occurrence of invertebrates in feral cat dietary studies by invertebrate family and the total number of individuals consumed.

Supplementary Table S3 provides a comparison of the frequency of occurrence of invertebrates in dietary samples from studies of three co-occurring mammalian predators in Australia; the feral cat, European red fox, and dingo.

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Table 1. The relative importance of variables from models predicting invertebrate frequency of occurrence.

Relative variable importance values (w_+) and the number of models containing the variable (N, in parentheses) derived from model-averaging (95% confidence model set of binomial GLM's modelling the effect of these variables on the frequency of occurrence of invertebrates [total and major orders] in feral cat diet). Highly influential variables are those with w+ ≥ 0.73, indicated in bold. Variable definitions: Rainfall – mean annual rainfall; Temperature – mean annual temperature; Rainfall : Temperature – interaction of mean annual rainfall with mean annual temperature; Tree cover – mean percentage tree cover within a 5km radius; Island size index – index of island size where the mainland sites (with area ≥10,000 km^2) had an index of 0 and islands <10,000 km^2 had negative values; Ruggedness – topographic ruggedness (standard deviation of elevation within a 5km radius).

	w_+ (N)						
Variable	Total invertebrates	Orthoptera (crickets and grasshoppers)	Chilopoda (centipedes)	Coleoptera (beetles)	Lepidoptera (butterflies and moths)	Scorpionida (scorpions)	Araneae (spiders)
Rainfall	**1.00 (26)**	0.38 (12)	0.27 (16)	**0.75 (17)**	0.56 (11)	**0.73 (19)**	0.16 (3)
Temperature	0.36 (14)	0.35 (14)	0.31 (15)	0.34 (13)	**0.85 (13)**	**1.00 (32)**	**1.00 (11)**
Rainfall : Temperature	**1.00 (26)**	0.02 (1)	0.02 (3)	0.08 (4)	0.06 (2)	0.14 (6)	0.11 (2)
Tree cover	**0.84 (15)**	0.47 (15)	**0.94 (29)**	**0.73 (15)**	0.45 (11)	0.26 (12)	**0.75 (8)**
Island size index	0.27 (13)	0.34 (11)	0.26 (17)	0.30 (11)	**0.73 (10)**	0.28 (14)	0.23 (3)
Ruggedness	0.26 (10)	**0.84 (16)**	0.34 (14)	0.22 (10)	0.24 (6)	0.37 (15)	**0.73 (7)**

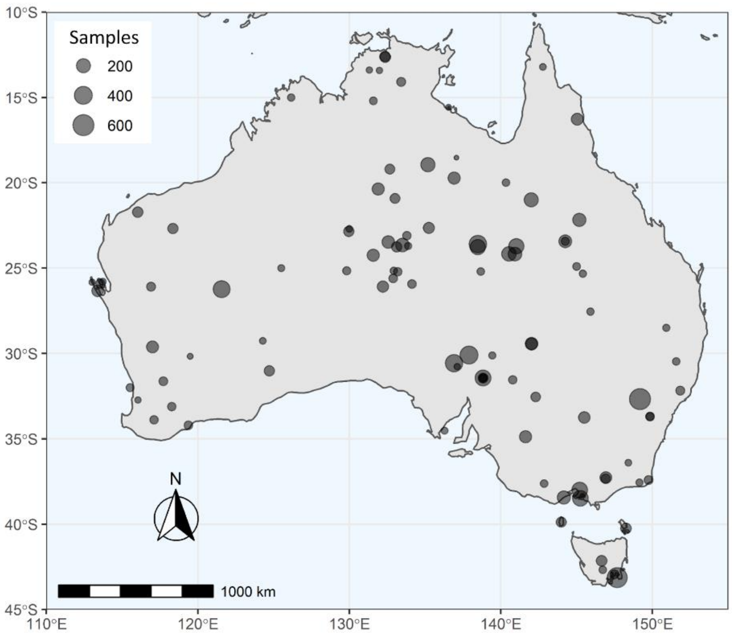


Fig. 1 Location of 87 cat dietary studies collated in this study. Circle size corresponds with sample size at each study site. Christmas Island (n = 187) and Macquarie Island (n = 756) are not shown.

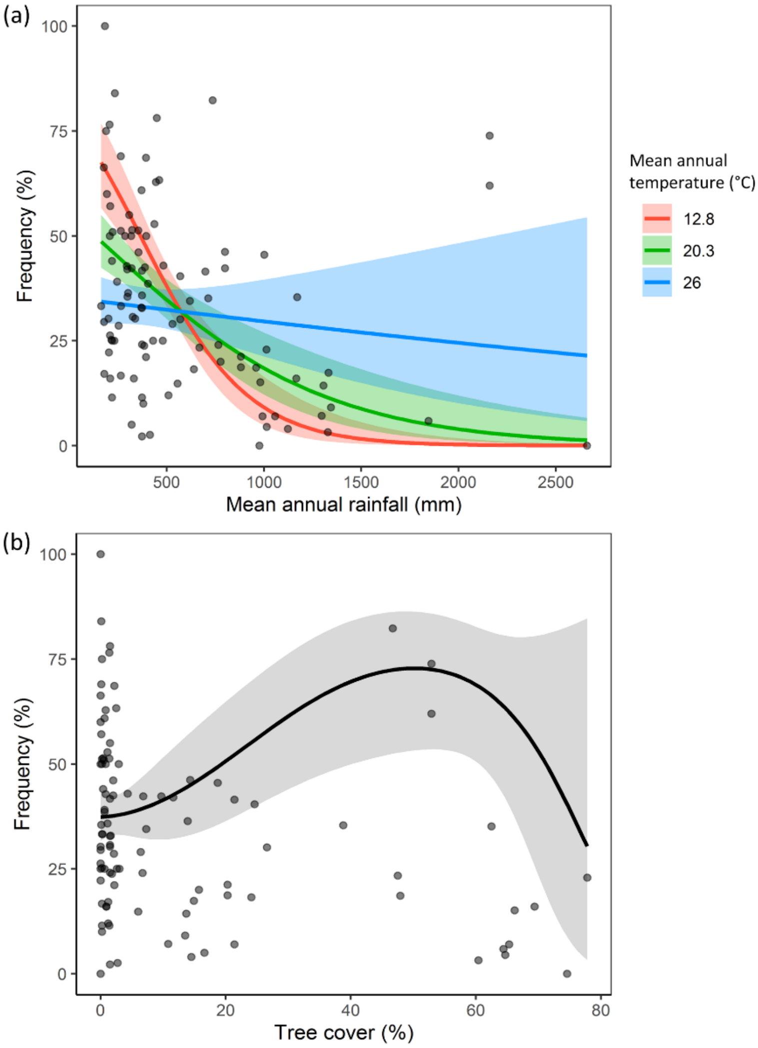
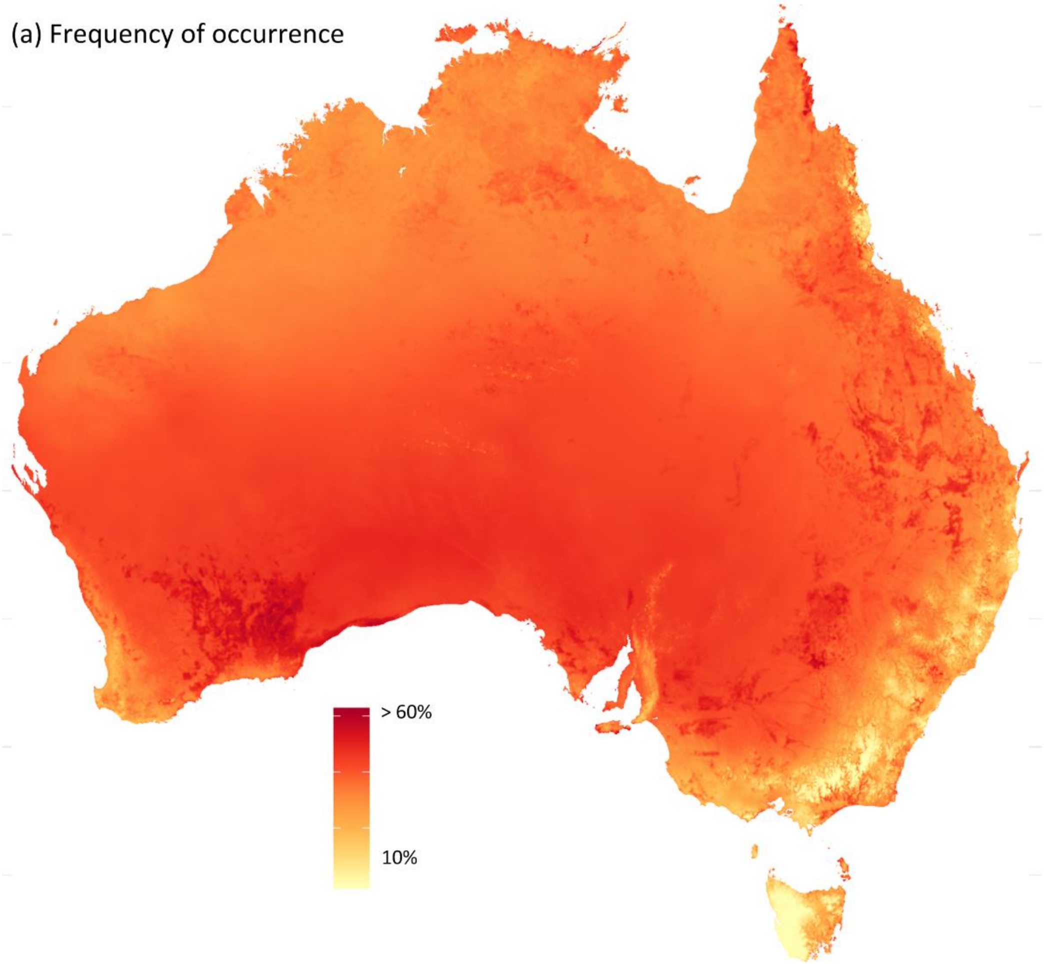


Fig 2. The frequency of occurrence of invertebrates in feral cat diet in relation to (a) mean annual rainfall by mean annual temperature, and (b) tree cover in Australia. Only highly influential variable relationships are shown (see Table 1), as derived from model predictions while holding other explanatory variables constant at their median level. The interaction between mean annual rainfall and temperature is shown by red and blue lines (and bands) representing model fit (and 95% confidence intervals) at first and third quartile levels of temperature respectively, and the green line (and band) is model fit (and 95% confidence intervals) at median temperature. Model fit for tree cover is shown by a continuous black line and the 95% confidence interval is represented by a grey band. Grey circles indicate observed data values and darker circles indicate repeated observations at the same point.

(a) Frequency of occurrence



(b) Consumption rate

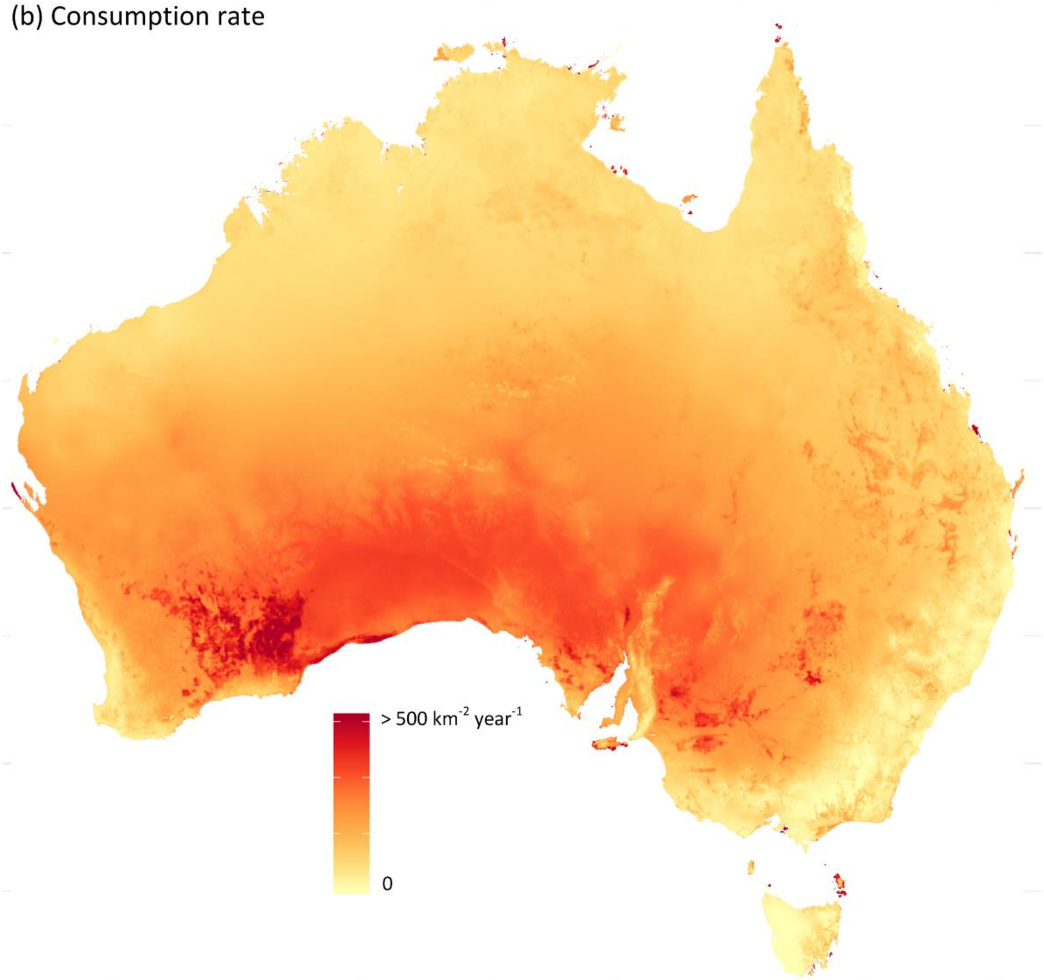


Fig. 3. Model projections of: (a) the frequency of occurrence (%) of invertebrates in feral cat diets, and (b) the rate of consumption of invertebrates by feral cats (km^{-2} $year^{-1}$) in largely natural environments throughout Australia.

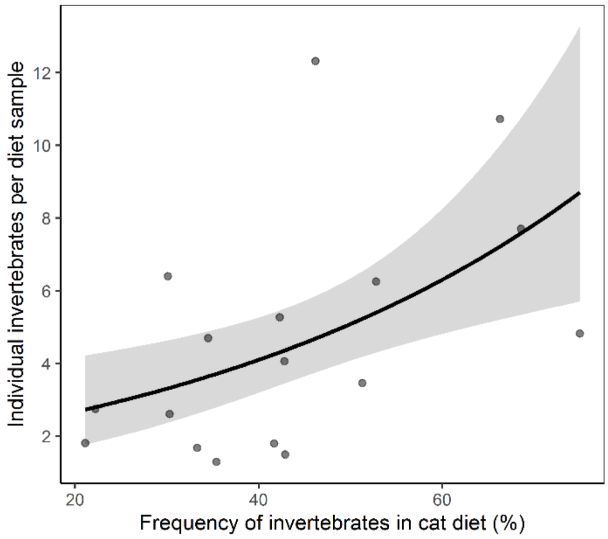


Fig 4. The modelled relationship between the number of individual invertebrates per cat sample containing invertebrates and the frequency of occurrence of invertebrates in feral cat dietary studies. Model fit is shown by a continuous black line and the 95% confidence interval is represented by a grey band. Circles indicate observed data values.

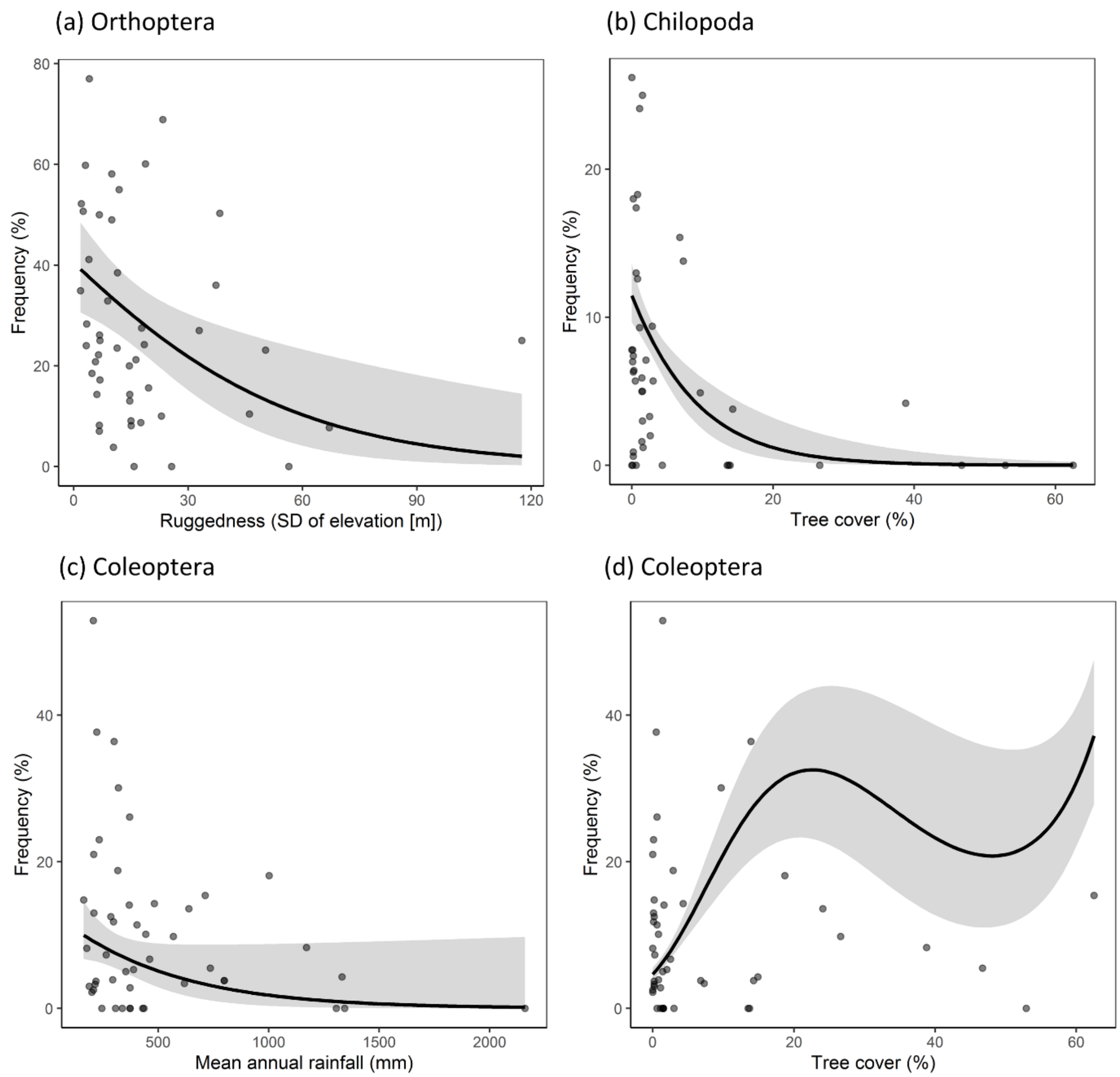


Fig 5. The frequency of occurrence of (a) Orthoptera (crickets and grasshoppers), (b) Chilopoda (centipedes), and (c, d) Coleoptera (beetles) in feral cat diet in relation to topographic ruggedness, tree cover and mean annual rainfall in Australia. Only highly influential variable relationships are shown (see Table 1), as derived from model predictions while holding other explanatory variables constant at their median level. Continuous black lines represent model fit and the 95% confidence interval is represented by a grey band. Grey circles indicate observed data values and darker circles indicate repeated observations at the same point.