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ORIGINAL PAPER

Fragments maintain similar herpetofauna and small mammal richness and diversity to continuous habitat, but community composition and traits differ

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Abstract

Context Human disturbance has transformed ecosystems globally, yet studies of the ecological impact of landscape modification are often confounded. Nonrandom patterns of land clearing cause differing vegetation types and soil productivity between fragments in modified landscapes and reference areas—like national parks—with which they are compared.

Objectives We sought to explore the influence of land modification on herpetofauna and small mammal communities using multiple biodiversity measures—species richness and diversity, individual species abundance, and community composition. We also aimed to investigate the role of traits such as diet, habitat breadth, and litter size in moderating species responses to land modification.

Methods We established 100 sampling sites to survey herpetofauna and small mammals in 11 fragments in an agricultural landscape compared to 11 ecologically equivalent 'pseudo-fragments' in a nearby national park in south-eastern Australia. We selected pairs of fragments and pseudo-fragments of the same size and vegetation type, and used identical survey methods to sample pairs simultaneously, thereby controlling for numerous confounding factors, such as differing vegetation type, weather, and survey effort.

Results Species richness and diversity were similar between fragments and pseudo-fragments. Despite this, we found community composition differed markedly—driven by the varying responses of individual species—indicating a shift in fauna communities

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associated with land modification. Fossorial habit, omnivorous diet, and broad habitat requirements led to higher abundance in fragments whilst arboreality, carnivorous diet, and narrow habitat requirements led to higher abundance in pseudo-fragments.

Conclusions Although fragments hold similar numbers of species to continuous areas, they contain distinct and novel communities, and sustain high abundances of some species. These diverse communities are dominated by native species, including threatened species, and their distinctive composition is shaped by traits conducive to persistence amidst land modification. These novel communities may provide a reservoir of resilience in the face of environmental change and should be viewed as complementary to conservation areas.

Keywords Community composition · Habitat fragmentation · Habitat loss · Patch dynamics · Species assemblages · Traits

Introduction

Habitat loss is the most pervasive threat to global biodiversity, driven primarily by the conversion of natural landscapes for agriculture and urbanisation (Powers and Jetz 2019). With over half of all ice-free land on Earth converted for agriculture (Hooke et al. 2013), conservation must occur within modified landscapes if we are to address the present 'extinction crisis' (Dirzo et al. 2022). Critical to informing conservation actions in these landscapes is the identification and quantification of the impacts of land modification. Overwhelmingly, native species richness is the response metric through which the effect of land modification on fauna is measured, with a common pattern of reduced richness in modified landscapes (Newbold et al. 2015; Thompson et al. 2016; Cordier et al. 2021). However, species richness is not always a reliable indicator of biodiversity (Fischer and Lindenmayer 2007). For example, richness might remain the same after land modification due to the immigration of overabundant generalist species, masking the loss of rare, endemic species (Matthews et al. 2014).

The 'habitat amount hypothesis' contends that species richness in fragments is driven by the 'sample area effect', where richness is primarily determined by the area of habitat in the local landscape (i.e., the sample area represented by the total habitat surrounding a sample site; Fahrig 2013). Fahrig (2013) advocates for the comparison of fragments with equal-sized areas but within a region of continuous habitat (hereon referred to as 'pseudo-fragments'; sensu MacNally and Bennett 1997). Though it has since been conceded that such comparisons do not directly test the habitat amount hypothesis (Fahrig 2021), these comparisons are nevertheless valuable in exploring the biodiversity value of fragments. Due to the sample area effect, species richness is expected to decline proportionally to reduction in fragment size purely as a function of habitat loss, rather than fragmentation. In contrast, the 'island biogeography theory' contends that individual fragment size and isolation determine species richness through demographic effects such as reduced immigration, increased inbreeding depression and elevated extinction in small, isolated fragments (Macarthur and Wilson 1967). This theory predicts a disproportionate reduction in species richness as fragment size decreases. Therefore, the mechanism driving richness patterns can be tested by comparing the slopes of the species-area curve between fragments and pseudo-fragments. "The sample area effect alone predicts that the species–area relationship for habitat patches should be lower, but have the same slope, as the relationship for sample areas within continuous habitat" (Fahrig 2013). Whereas, under island biogeography theory "the species–area relationship for habitat patches should be steeper than for sample areas within continuous habitat" (Fahrig 2013).

Community composition, which incorporates the relative abundances of all species detected at a site, provides another lens through which the effect of landscape modification can be viewed. Compositional differences can occur despite similar richness, providing insight into subtle changes in the structure of a community (Kay et al. 2018). Community composition is driven by individual species responses to modification which are, at least partly, mediated by ecological and life history traits (Henle et al. 2004; Keinath et al. 2017). Under the 'landscape-moderated functional trait selection hypothesis' (Tscharntke et al. 2012), species trait selection shapes the trajectory of community assembly. Traits such as generalist dietary and habitat requirements, high dispersal ability, and high fecundity are thought to be advantageous whilst large body size, specialist dietary and habitat requirements, and complex social structure are disadvantageous in fragments (Henle et al. 2004; Cardillo et al. 2005; Michael et al. 2015; Keinath et al. 2017).

While the management emphasis in modified landscapes typically prioritises protecting large sections of remnant vegetation, growing evidence demonstrates the value of small fragments for wildlife conservation (Tulloch et al. 2016; Riva and Fahrig 2022). Indeed, a global meta-analysis revealed that small, isolated fragments tended to have higher conservation value than similarly sized areas in continuous tracts of vegetation (Wintle et al. 2019). Similarly, an analysis of 32 datasets comparing species richness across small and large fragments found small outperformed large in 25 of 32 instances, and no instance of large fragments outperforming small (Riva and Fahrig 2022).

The disproportionate importance of small fragments is likely due to several factors. In agricultural landscapes, remnant fragments often occur in flat, fertile landscapes that have been selectively cleared due to their high productivity (Watson 2011; Maron et al. 2012; Simmonds et al. 2017). Consequently, their host biota are quite distinct from sites with steep terrain or poor soils, where larger areas set aside for conservation (e.g., conservation reserves) tend to exist, due to their low value to agriculture (Watson et al. 2014; Venter et al. 2018; Engert et al. 2023). Thus, small fragments may be all that remains of heavily cleared, but highly productive, ecosystem types. This creates problems when comparing ecological communities between fragments and nearby ‘reference areas’ set aside for conservation, as such comparisons are often confounded by factors, such as vegetation type, that differ between fragments and reference areas because of non-random land clearing (Maron et al. 2012; Simmonds et al. 2017). Furthermore, land modification alters ecological processes in remnant fragments. For example, fire is typically excluded from fragments and many fragments are exposed to livestock grazing, both of which alter fragment vegetation. Additionally, species detectability can vary according to circadian rhythms, seasonality, weather conditions, and survey method, potentially further confounding comparisons (Boulinier et al. 1998). Therefore, to make fair comparison between fragmented and non-fragmented communities requires standardized survey design, methods and sampling effort to limit temporal and spatial confounds from influencing inference.

We investigated the occurrence of herpetofauna and small mammals, as well as the activity of introduced predators, in woodland fragments within an agricultural matrix compared to ecologically equivalent pseudo-fragments in a nearby national park in south-eastern Australia. We endeavoured to control for external factors that typically vary in fragmentation studies (e.g., vegetation type), to capture the effect of land modification alone. We sought to answer the overarching question: do fauna communities differ between isolated fragments and continuous pseudo-fragments of habitat? Our approach considered multiple biodiversity measures—species richness and diversity, community composition and individual species abundance—along with trait data to explore the effect of land modification. In accordance with both the habitat amount hypothesis and island biogeography theory, we expected lower species richness and diversity in fragments compared to pseudo-fragments. Consistent with the ‘landscape-moderated functional trait selection hypothesis’, we predicted communities in fragments and pseudo-fragments to differ in composition owing to the varying response of individual species, mediated by traits. We predict generalist species to show increased abundance in response to modification whilst specialist species will show decreased abundance.

Materials and methods

Study area

The study was undertaken within the Little Desert National Park and surrounding agricultural land in western Victoria, Australia (Fig. 1A). The area receives an average of 449 mm annual rainfall with mean maximum temperature of 31.3 °C in January, 14.0 °C in July and mean minimum temperature of 13.9 °C and 4.5 °C, respectively (Bureau of Meteorology, http://www.bom.gov.au/climate/data/). The landscape is characterised by sandy soils and contains a series of undulating dunes and swales, and expansive plains. Three vegetation communities dominate the landscape—Lowan Sands Mallee, occurring on light sandy soil, dominated by desert stringybark (*Eucalyptus arenacea*), reaching 5–10 m, with a dense heathy understory usually containing grass trees (*Xanthorrhoea australis*). Sandstone Ridge

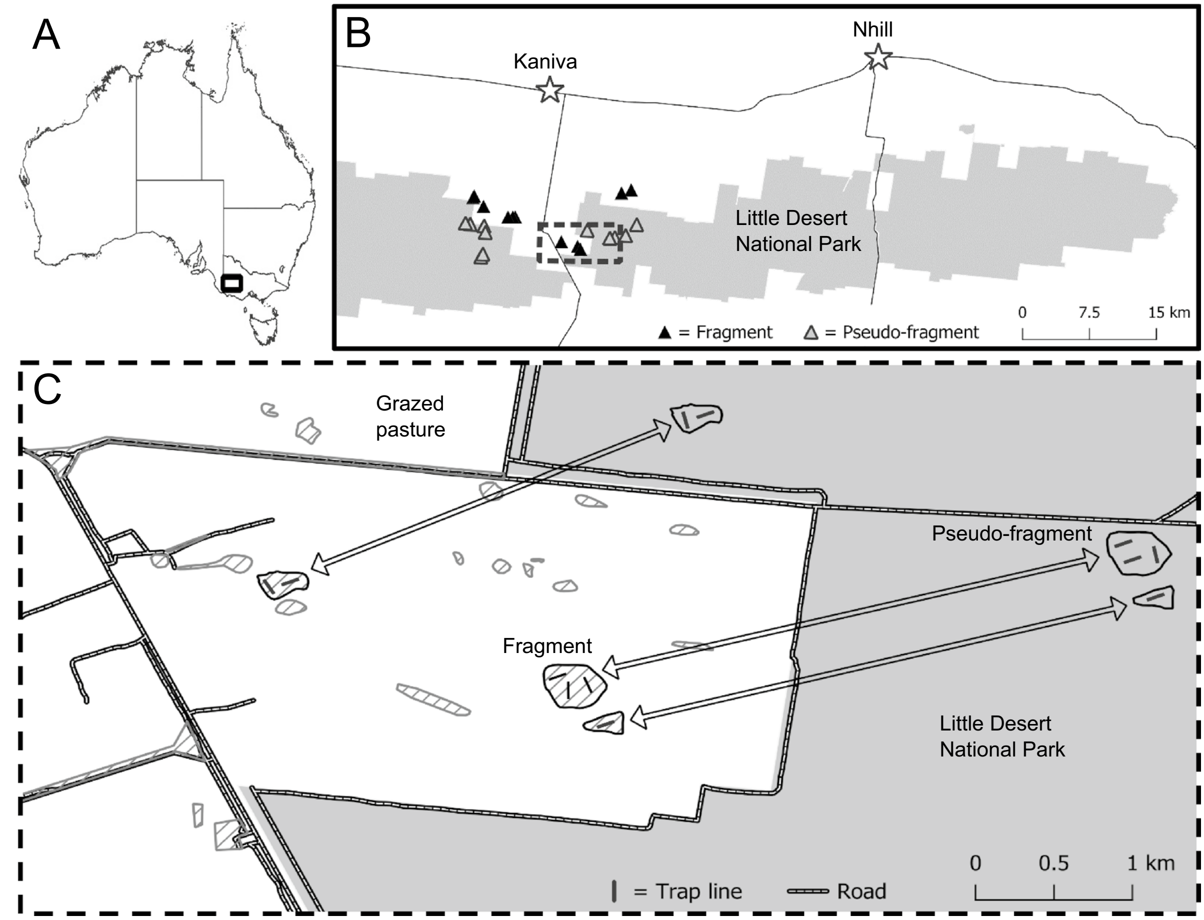

Fig. 1 **A** National scale: study area location within Australia, **B** regional scale: study fragments (solid triangles) and pseudo-fragments (hollow triangles) across the Little Desert National Park and surrounds, and **C** landscape scale: study fragments in the agricultural landscape and paired pseudo-fragments (connected with arrows) in the adjacent national park showing proportional sampling. Continuous vegetation of the national park is shaded grey, whilst fragments of remnant native vegetation in the agricultural landscape are hashed grey

Shrubland, occurring on sandy sandstone outcrops, contain sparse multi-stemmed eucalypts (predominantly ridge-fruited mallee, *E. costata,* and slender-leaf mallee, *E. leptophylla*) reaching < 5 m high, and abundant mid-storey shrubs (broom honey-myrtle, *Melaleuca uncinata,* violet honey-myrtle, *M. wilsonii,* and broom baeckea, *Hysterobaeckea behrii*). Yellow Gum Woodland exists over clay soils, with yellow gum (*E. leucoxylon*) the main tree species reaching > 10 m, and a variety of shrubs and grasses creating a relatively open understory.

Outside the national park, agriculture (predominantly sheep grazing and cropping) is widespread in the region. Early clearing by European colonists began in the late 1800s removing much of the native vegetation, particularly on the more productive 'Wimmera black soils' (Landt 1961). As has happened across the world (Watson et al. 2014; Simmonds et al. 2017; Venter et al. 2018), vegetation communities on fertile soils were selectively cleared, leaving the majority of native vegetation remaining on less fertile, sandy soils. From the 1960s onwards, agriculture expanded into less fertile, sandy soils abutting the Little Desert National Park (Landt 1961). Small fragments of vegetation were left uncleared to provide shelter for livestock, so that farms comprise a mosaic of patches of remnant vegetation of differing shape and size, surrounded by pasture or cropland. These fragments support the same soils and vegetation types to the adjacent national park, providing an opportunity to test for the effect of land modification without the confounding effects of vegetation type and variation in resource availability and productivity. Increasingly, intensification of agricultural practices in the region has diminished remnant vegetation in farming landscapes (Maron and Fitzsimons 2007).

Experimental design

We sampled 11 matching pairs of fragments ($n = 11$) and pseudo-fragments ($n = 11$), 1–10 ha in size. Each fragment is a patch of remnant vegetation (isolated 11–60 years ago) surrounded by cleared grazing land. Using geographic information systems and ground-truthing, each fragment was paired with a pseudo-fragment—an area of the same size as the fragment, comprised of the same vegetation type, but embedded within the continuous habitat of the national park (MacNally and Bennett 1997; Deacon and Mac Nally 1998; Johnstone et al. 2010, 2012, 2014).

Each paired fragment and pseudo-fragment were selected to be as similar as possible, differing only in landscape context (i.e., isolated fragment vs. continuous pseudo-fragment) and land-use (Fig. 1C). Fire history was considered in pair selection to account for the effect of post-fire succession on biotic communities (Nimmo et al. 2013; Haslem et al. 2011). No fire had occurred in any of the fragments since the time of clearing according to the landholders. For pseudo-fragments, we used the "Fire History Records of Fires across Victoria" dataset (DEECA 2023). The region has experienced numerous large wildfires and frequent planned burns in recent years. Therefore, we focussed on the longest unburnt areas available to locate pseudo-fragments (9/11 last burnt > 40 years ago, the remaining two burnt 25 and 28 years ago respectively), so that fire history of pseudo-fragments matched fragments (all last burnt > 40 years ago) as closely as possible. Fragments were periodically exposed to sheep grazing, although two of the 11 fragments were fenced off excluding sheep (but subject to historic grazing) but not impeding the movement of the herpetofauna and small mammals studied.

The relatively small size of the fragments and pseudo-fragments (< 10 ha) allowed us to survey them intensively (each surveyed ~ 30 times), reducing the likelihood of false negatives. An area-proportionate sampling approach was undertaken in which the survey effort (the number of trap lines) was dependent on fragment size. Specifically, for every hectare, each fragment contained one pitfall line, a 30-m-long aluminium flywire drift fence running through three 20-L buckets and two double-ended funnel traps. In addition, two artificial refuge stations were established adjacent to each trap line, each composed of a double-stack of 1 m^2 sheets of corrugated tin, and two terracotta roof tiles placed on the ground. This multi-method capture design was used to reduce method-related capture bias for different species, maximizing the detection of target species. Trap lines were separated by at least 50 m, making it unlikely for most target species to visit multiple trap lines (Pulsford et al. 2018).

Our paired design allowed sampling in fragments and pseudo-fragments to be almost identical, thereby controlling for sampling bias and detectability. Between November 2021 and January 2022, all traps were open for three blocks (one per month) of five consecutive days and nights except when temperature exceeded 35 °C or predicted daily rainfall exceeded 5 mm. Trap nights (calculated as the total number of 24-h periods each pitfall and funnel trap was open for plus the number of times artificial refuges were checked) ranged from 101 in the smallest fragments to 960 in the largest. Traps were checked twice a day, at dawn and dusk, and refuge stations checked twice each trapping block. Paired fragments were always trapped on the same days at approximately the same time by two separate teams.

Vegetation surveys

To assess habitat structure, vegetation surveys were conducted at each of the 100 trap lines. Habitat structure was measured using vertical structure poles at 1-m intervals along a 30-m transect run parallel to the drift fence, 5 m away. At each metre along the transect, leaf litter depth was given a rating between 0 (bare ground) and 4 (5 cm +), and the incidence of vegetation touching the structure pole was recorded for low (0–0.5 m), mid (0.5–1.0 m), high (1–2 m) and canopy (2 m +) strata. Coarse woody debris volume was recorded by measuring length and diameter of logs that fell within 5 m either side of the transect. The closest six trees of the dominant species in the area were measured for diameter at breast height (Fig. 2).

Camera trapping

Camera traps were deployed at each fragment and pseudo-fragment to provide an index of activity for two introduced predators prominent in the region: the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*). Small fragments (0–3 ha) contained one camera, medium fragments (4–6 ha) two cameras and large fragments (7–10 ha) three cameras which collected images semi-continuously throughout the duration of the study. Cameras used were all of the same model (Swift Enduro), were set to medium sensitivity, and to capture five images after each trigger with no delay. Cameras were placed at waist height, facing downwards to a focus point on the ground 1.5–2 m from the tree the camera was placed on. Cameras were initially baited (with a punctured tin of sardines) whilst traps were inactive and unbaited during trapping to avoid attracting predators to vulnerable animals in traps.

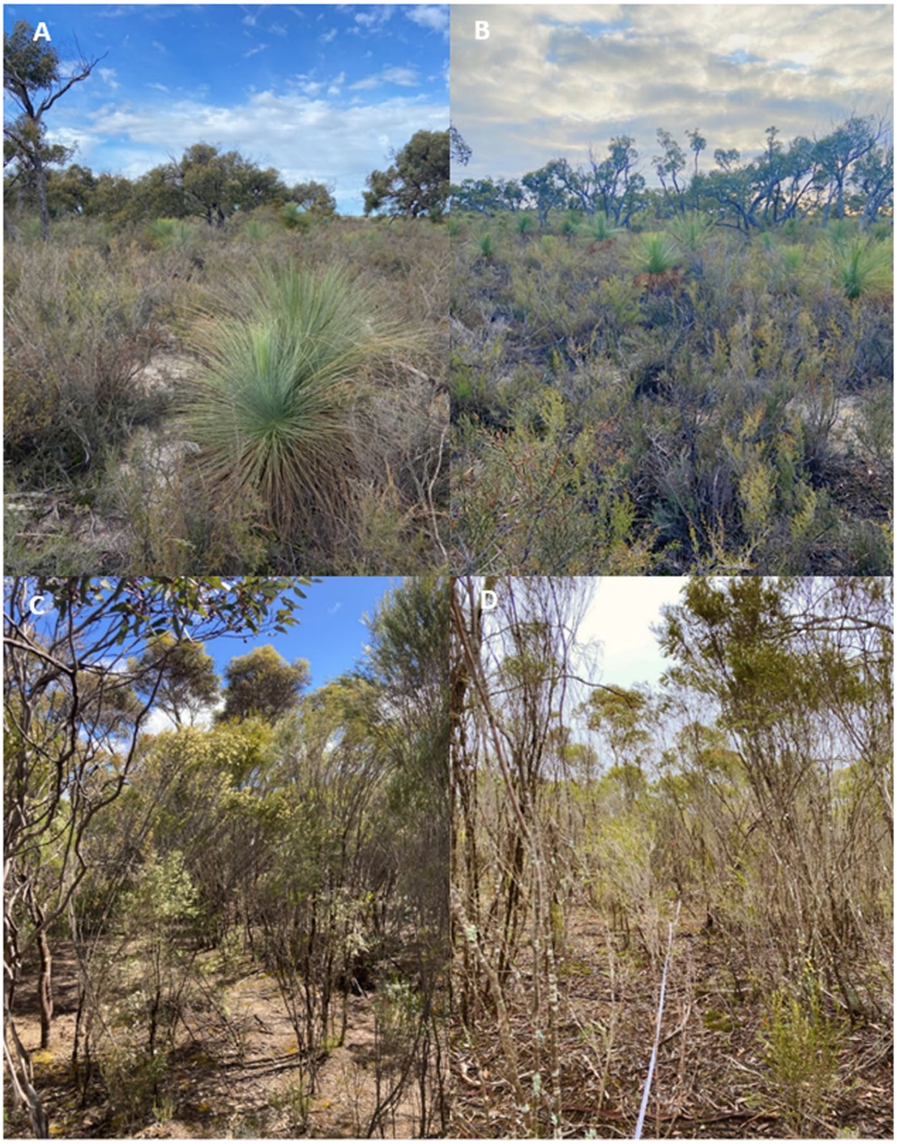

Fig. 2 Vegetation similarity between paired fragments and pseudo-fragments: **A** Lowan Sands Mallee fragment, **B** Lowan Sands Mallee pseudo-fragment, **C** Sandstone Ridge Shrubland fragment, and **D** Sandstone Ridge Shrubland pseudo-fragment

Statistical analyses

All analyses were performed in R (R Core Team 2023).

Does vegetation structure differ between fragments and pseudo-fragments?

We used generalised linear mixed effect models (GLMMs) using the "lme4" package (Bates et al. 2015) to compare vegetation structure between fragments and pseudo-fragments. The data was divided into vegetation types to enable a comparison between the attributes of vegetation in fragments and those in pseudo-fragments, controlling for vegetation type. Structural complexity at low, mid, high and canopy strata were modelled as the proportion of times along the transect that vegetation touched the vertical structure pole for each stratum, assuming a binomial error distribution. Leaf litter depth, coarse woody debris volume, largest tree (diameter at breast height) and mean tree size (diameter at breast height) were modelled assuming a Gaussian distribution. Each of these vegetation metrics mentioned above were modelled in turn as the response variable, whilst fragment type was specified as a categorical fixed effect with two levels (fragment, pseudo-fragment) and fragment ID specified as a random effect to account for non-independence of sites (transects) within fragments.

Does species richness and diversity differ between fragments and pseudo-fragments?

Species richness (total number of species) and Shannon's diversity index (a measure of diversity incorporating species richness and evenness) were calculated for each fragment and pseudo-fragment. We used raw rather than standardised values because: (1) our study design ensured almost identical survey effort across paired fragments and pseudo-fragments, (2) low sample sizes resulting from lower survey effort at smaller fragments and pseudo-fragments resulted in standardised estimates with high levels of uncertainty. Cross-sample singletons and doubletons (i.e., species that were recorded only once or twice across all sampling) were excluded from all analyses as their removal has shown to decrease error rate and improve accuracy of diversity metrics (Allen et al. 2016).

Species richness and diversity values were modelled against the predictor variables fragment type (fragment vs. pseudo-fragment), fragment size (1–10 ha), and their interaction term, using generalised linear models (GLMs) assuming a Gaussian error distribution. Here, we define 'fragment size' as the area of the fragment and the equivalent area sampled for their paired pseudo-fragments. Models were ranked according to Akaike's Information Criterion adjusted for small sample sizes (AICc) and coefficients (and 85% CIs; Arnold 2010) reported for all supported models (delta AICc < 2; Burnham and Anderson 2004).

Does community composition differ between fragments and pseudo-fragments?

To examine how land modification affects community composition, we used Permutation Multivariate Analysis of Variance (PERMANOVA) from the "vegan" package (Dixon 2003). Species abundances were used to calculate Bray–Curtis dissimilarity measures for each of the fragments and pseudo-fragments. Significance values were calculated based on 999 unrestricted permutations of the raw data. Differences in community structure between fragment types were visualised through non-metric multi-dimensional scaling (nMDS). Indicator species analysis was conducted using the "indicspecies" package (Cáceres and Legendre 2009) to identify species characteristic of fragments and pseudo-fragments respectively.

To explore herpetofauna and small mammal community compositional differences further, we modelled species abundance (total number of individuals of each species captured in each fragment/pseudo-fragment) and incidence (proportion of trap lines occupied per fragment/pseudo-fragment) in relation to fragment type and fragment size. Generalised linear models were performed for species which were captured 11 or more times (equal to half the total number of fragments/pseudo-fragments; Williams et al. 2012). Abundances were modelled assuming a Poisson error distribution and with a log link function. Species' incidence was modelled as the number of success (trap lines occupied per fragment) and failures (trap lines unoccupied per fragment) within a fixed number of Bernoulli trials (total number of trap lines per fragment), assuming a binomial error distribution and with a logit link function. Four models including the variables fragment type, fragment size, and the interaction term were fit. Due to evidence of overdispersion in global models for some species, model selection was performed according to QAICc, thereby accounting for potential overdispersion. Supported models (delta QAICc < 2) were fit specifying a quasipoisson or quasibinomial error distribution (Burnham and Anderson 2004).

Do traits mediate species abundance between fragments and pseudo-fragments?

Traits were considered for only our most abundant class—reptiles—as we recorded too few amphibian and mammal species (2 and 5 species respectively) to warrant their inclusion. Trait data (Table S7) was collated from a global trait database (Meiri 2018), complemented by a comprehensive field guide to the region (Robertson and Coventry 2014), and included litter size, mass, snout-vent length, taxonomic family, diet, habit, activity period, leg development, and temperature regulation. Additionally, habitat breadth was calculated as a measure of habitat specialisation following established methods (Ducatez et al. 2014; Lettoof et al. 2023) using the IUCN Red List database (IUCN 2023).

Cohen's d effect sizes were calculated for each species, with 95% confidence intervals from 1000 bootstrap samples, to estimate the magnitude of difference in abundance between fragments and pseudo-fragments. A multiple regression analysis was then performed to investigate the relationship between species traits and calculated effect sizes. We fit models including all combinations (without interactions) of the traits previously listed. The confidence intervals of effect sizes were included in the model via inverse variance weighting using the "weights" argument. Models were ranked according to AICc and coefficients (and 85% CIs) reported for supported models (delta AICc < 2).

Does introduced predator activity differ between fragments and pseudo-fragments?

Site-specific relative abundance indices were calculated for the introduced predators, red fox and feral cat. We considered detections > 30 min apart to be a separate event to account for the same animal being detected multiple times in the same visit (Cunningham et al. 2018). We used generalised linear models (GLMs) using the "lme4" package (Bates et al. 2015) with relative abundance indices for each fragment/pseudo-fragment as the response variable and fragment type (fragment vs. pseudo-fragment) as the predictor variable to determine the influence of fragment type on predator activity.

Results

Does vegetation structure differ between fragments and *pseudo*-fragments?

Vegetation structure was similar between paired fragments and pseudo-fragments with 10 out of 14 metrics measured showing no significant difference between fragment types. Structural complexity at low (< 0.5 m) and medium (0.5–1 m) strata were similar across fragment types (Table S1, Fig. 3C and D). However, despite selecting pseudo-fragments to be as similar as possible to fragments, the latter showed higher structural complexity within the high (1–2 m) and canopy (> 2 m) strata (Table S1, Fig. 3E and F), and deeper leaf litter (Table S1, Fig. 3B). The volume of coarse woody debris (Table S1, Fig. 3A) and tree size (Table S1) were similar between treatments, except for one species of tree, *E. leptophylla*, which were larger in fragments.

Does species richness and diversity differ between fragments and *pseudo*-fragments?

Across 9,618 trap nights, a total of 1,736 individuals from 19 reptile species, five mammal species, and two amphibian species (there were likely three but due to the difficulty of distinguishing between *Neobatrachus pictus* and *N. sudellae*, these two species were combined) were recorded. In total, 867 individuals were sampled from 25 species in fragments and 869 individuals from 23 species in pseudo-fragments (Table 1). Three species were found exclusively in fragments (*Echiopsis curta*, *Notechis scutatus*, *Sminthopsis crassicaudata*) whilst one species was found exclusively in pseudo-fragments (*Varanus rosenbergi*). The most abundant species were *Morethia obscura* (383 captures, 22.06% of total captures),

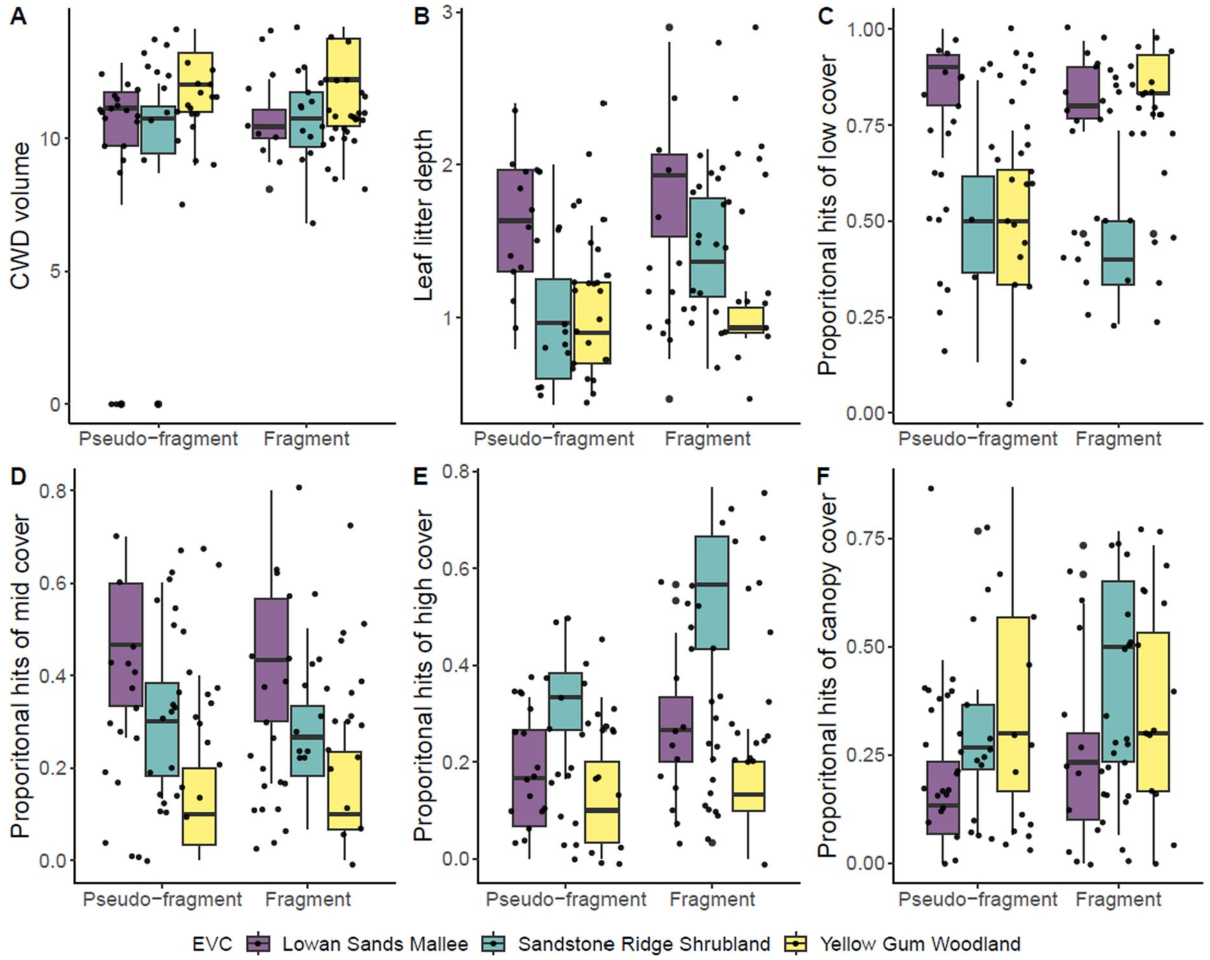

Fig. 3 Vegetation metrics across fragment type and Ecological Vegetation Class (EVC) categories: **A** volume of coarse woody debris (log(cm^3)), **B** leaf litter depth rating, and structural complexity of low (0–0.5 m; **C**), mid (0.5–1.0 m; **D**), high (1–2 m; **E**) and canopy (>2 m; **F**) strata. Black dots represent data values from each transect

Ctenotus robustus (197, 11.35%), *Ctenotus orientalis* (193, 11.12%), and *Pseudomys apodemoides* (175, 10.08%). Pitfall traps were the most successful survey method recording 1,191 animals (0.33 animals/trap night). Funnel traps captured 501 animals (0.21 animals/trap night), whereas tin stacks (39 captures, 0.03 animals/trap night) and roof tiles (5 captures, 0.002 animals/trap night) accounted for far fewer animals.

Species richness ranged from four to 20 species per fragment/pseudo-fragment. The most parsimonious model included only fragment size (Table S2), while the null model was also supported. Parameter estimates showed that species richness increased with fragment size (Table S3). We observed no evidence of an ‘island effect’ on species richness where the species-area curve for fragments would be steeper compared to pseudo-fragments (Fig. 4).

Shannon’s diversity estimates in fragments and pseudo-fragments ranged from 0.75 to 2.39. Two models received substantial support: the null model, and the model including fragment size (Table S2). Parameter estimates suggest there was a small positive effect of fragment size on diversity (Table S3).

Does community composition differ between fragments and *pseudo*-fragments?

Community composition differed significantly across fragment types (PERMANOVA: $R^2 = 0.217$, d.f. = 1, $p < 0.001$). The ordination showed a clear separation

Table 1 Total abundance (number of fragments/pseudo-fragments detected at) for each species recorded in the study

Common name	Scientific name	Code	Pseudo-fragment	Fragment	Total
Agamidae					
Mallee Tree Dragon	*Amphibolurus norrisi*	AmpNor	23 (9)	2 (2)	25 (11)
Painted Dragon	*Ctenophorus pictus*	CtePic	35 (7)	22 (4)	57 (11)
Eastern Bearded Dragon	*Pogona barbata*	PogBar	4 (3)	1 (1)	5 (4)
Diplodactylidae					
Eastern Stone Gecko	*Diplodactylus vitattus*	DipVit	4 (2)	5 (1)	9 (3)
Elapidae					
Bardick	*Echiopsis curta*	EchCur	0 (0)	1 (1)	1 (1)
Tiger Snake	*Notechis scutatus*	NotScu	0 (0)	1 (1)	1 (1)
Eastern Brown Snake	*Pseudonaja textilis*	PseTex	1 (1)	4 (4)	5 (5)
Mitchell's Short-tailed Snake	*Suta nigriceps*	SutNig	5 (5)	3 (3)	8 (8)
Gekkonidae					
Marbled Gecko	*Christinus marmoratus*	ChrMar	83 (10)	45 (7)	128 (17)
Pygopodidae					
Lined Worm-lizard	*Aprasia striolata*	AprStr	3 (3)	9 (5)	12 (8)
Common Scaly-foot	*Pygopus lepidopodus*	PygLep	9 (4)	2 (2)	11 (6)
Scincidae					
Spotted Ctenotus	*Ctenotus orientalis*	CteOri	90 (11)	103 (11)	193 (22)
Robust Ctenotus	*Ctenotus robustus*	CteRob	38 (2)	159 (10)	197 (12)
Delicate Skink	*Lampropholis delicata*	LamDel	71 (9)	68 (8)	139 (17)
South-eastern Slider	*Lerista bougainvilli*	LerBou	9 (5)	38 (10)	47 (15)
Common Dwarf Skink	*Menetia greyii*	MenGre	17 (6)	21 (6)	38 (12)
Shrubland Morethia	*Morethia obscura*	MorObs	210 (11)	173 (11)	383 (22)
Shingleback Lizard	*Tiliqua rugosa*	TilRug	1 (1)	11 (7)	12 (8)
Varanidae					
Heath Goanna	*Varanus rosenbergi*	VarRos	5 (3)	0 (0)	5 (3)
Burramyidae					
Western Pygmy-possum	*Cercartetus concinnus*	CerCon	19 (6)	28 (8)	47 (14)
Little Pygmy-possum	*Cercartetus lepidus*	CerLep	62 (10)	15 (5)	77 (15)
Dasyuridae					
Fat-tailed Dunnart	*Sminthopsis crassicaudata*	SmiCra	0 (0)	2 (1)	2 (1)
Muridae					
House Mouse	*Mus musculus*	MusMus	2 (2)	24 (7)	26 (9)
Silky Mouse	*Pseudomys apodemoides*	PseApo	134 (7)	41 (1)	175 (8)
Limnodynastidae					
Eastern Banjo Frog	*Limnodynastes dumerilii*	LimDum	21 (4)	77 (11)	98 (15)
Neobatrachus sp.	*Neobatrachus sp.*	NeoSp	23 (5)	12 (5)	35 (10)
Total			869 (11)	867 (11)	1736 (22)

between communities in fragments compared to pseudo-fragments (Fig. 5). Indicator species analysis found three lizard species (*C. robustus*, *Tiliqua rugosa*, *Lerista bougainvilli*), one frog species (*Limnodynastes dumerilii*) and one rodent species (*Mus musculus*) to be strongly associated with fragments. Conversely, one species of lizard (*Amphibolurus norrisi*), and one marsupial species (*Cercartetus lepidus*) were strongly associated with pseudo-fragments (Table 2). Abundance showed a significant association (85% CIs did not overlap zero) with fragment type for nine of the 18 species for which modelling

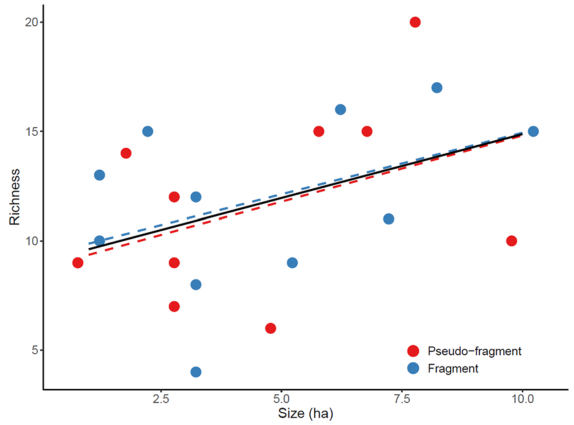

Fig. 4 The relationship between species richness and fragment size for fragments (blue) and pseudo-fragments (red). Dashed lines represent regression lines for fragments and pseudo-fragments individually, whilst the solid black line shows the overall regression line

was performed. Eleven of 18 species showed an association with fragment size whilst the interaction term between fragment type and fragment size influenced abundance for three of 18 species (Table 3).

For individual species abundances, model parameters identified the same five species as in indicator species analysis, and an additional legless lizard species (*Aprasia striolata*) to be positively associated with fragments (Table 4; Fig. 6A–C). The same two species identified by indicator species analysis as well as one legless lizard species (*Pygopus lepidopodus*) showed a significant negative association with fragments and, thus, a positive association with pseudo-fragments (Table 4; Fig. 6D, E). All 11 associations with fragment size were positive (abundance increased with fragment size). Findings were similar when using the proportion of survey lines (sites) occupied per fragment/pseudo-fragment as the response variable (Tables S4 and S5, Fig S1).

Do traits mediate species abundance in fragments and *pseudo*-fragments?

The only supported model explained the data well ($R^2 = 0.799$) and included three traits as predictor variables: diet, habit and habitat breadth (Table 5). Species with a carnivorous diet or semi-arboreal habit were more abundant in pseudo-fragments, whereas those with an omnivorous diet or fossorial habit were more abundant in fragments (Fig. 7; Table 6). Habitat specialists were more abundant in pseudo-fragments compared to habitat generalists which were more abundant in fragments.

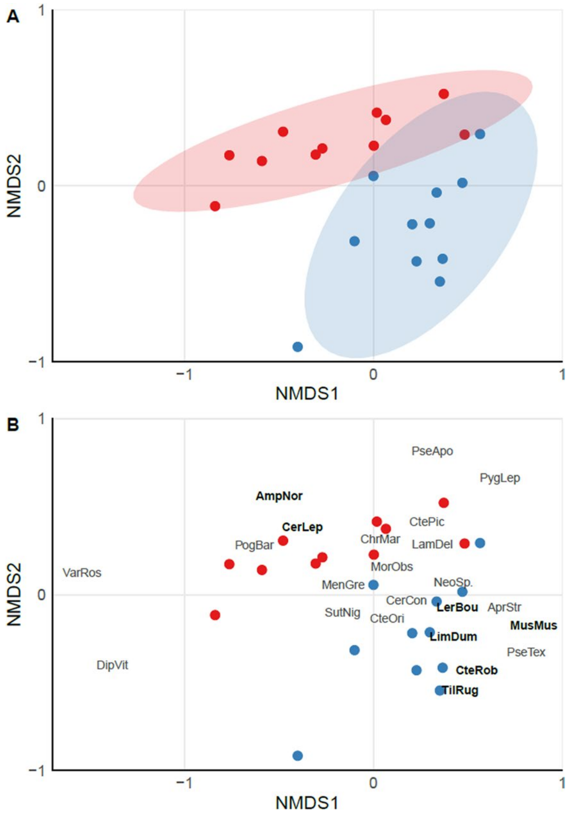

Fig. 5 The nMDS ordination showing: **A** the separation of community composition between fragments (blue) and pseudo-fragments (red). Each point represents a fragment/pseudo-fragment plotted on unobserved variables (NMDS1 and NMDS2) used to visualise dissimilarity between points. Ellipses show 95% confidence intervals. **B** Individual species' position according to the fragments/pseudo-fragments they occurred in (first 3 letters of genus and species; see Table 1 for species list). 'Indicator species' are shown in bold

Does introduced predator activity differ between fragments and *pseudo*-fragments?

Over 8,994 trap days, 310 fox detection events (271 in fragments and 39 in pseudo-fragments) and four cat detection events (one in a fragment and three in pseudo-fragments) occurred. Modelling was only performed for foxes due to low overall detection of cats. Fox activity was significantly higher in fragments

Table 2 Results of indicator analysis showing species associated with fragments and pseudo-fragments. Significant (95%) associations are shown in bold

	IndVal	p
Fragment-associated species		
Limnodynastes dumerilii	0.886	**0.009**
Lerista bougainvilli	0.857	**0.014**
Ctenotus robustus	0.857	**0.001**
Mus musculus	0.766	**0.048**
Tiliqua rugosa	0.764	**0.01**
Ctenotus orientalis	0.731	0.802
Cercartetus concinnus	0.658	0.404
Aprasia striolata	0.584	0.26
Menetia greyii	0.549	0.855
Pseudonaja textilis	0.539	0.324
Pseudo-fragment-associated species		
Amphibolurus norrisi	0.868	**0.002**
Cercartetus lepidus	0.856	**0.003**
Christinus marmoratus	0.768	0.128
Morethia obscura	0.74	0.651
Pseudomys apodemoides	0.698	0.08
Lampropholis delicata	0.646	0.812
Ctenophorus pictus	0.625	0.35
Neobatrachus sp.	0.547	0.622
Pygopus lepidopodus	0.545	0.218
Suta nigriceps	0.533	0.648
Varanus rosenbergi	0.522	0.219
Pogona barbata	0.467	0.469
Diplodactylus vitattus	0.284	1.000

compared to pseudo-fragments (Coefficient ± 85% CI = 1.16 [0.45–1.87], $R^2 = 0.23$; Table S6).

Discussion

Land clearing has transformed ecological communities worldwide, yet studies of the impact of landscape modification are often confounded by non-random patterns of land clearing. We compared communities of herpetofauna and small mammals of remnant fragments in modified landscapes to similar pseudo-fragments in continuous habitat. Total number of animals, species richness, and species diversity were similar between fragments and pseudo-fragments. Despite this, community composition differed between fragment types indicating a shift in fauna communities associated with land modification. Relative abundances of individual species show there are ‘winners and losers’ in modified landscapes as some species proliferate in fragments whilst others decline. We explore the influence of traits in determining a species’ response to land modification.

Does vegetation structure differ between fragments and *pseudo*-fragments?

Despite intentionally matching similar habitat across fragments and pseudo-fragments, vegetation surveys showed some significant differences between fragment types, including deeper leaf litter and more complex vegetation structure at higher strata for fragments. Abiotic factors, such as soil quality, typically differ between fragmented habitat and continuous habitat due to non-random land clearing (Simmonds et al. 2017; Maron et al. 2012), likely contributing to differing vegetation structure. Additionally, land clearing alters ecological processes by increasing edge effects, promoting weed invasion, encouraging grazing by domestic and native herbivores, and altering fire regimes. These effects combined mean that fragmented and continuous habitat are unlikely to be truly equivalent, despite their regular comparison in ecological research.

One possible explanation for the differences observed in our study, is that the absence of fire in fragments allowed leaf litter to accumulate and taller growth of large shrubs and trees. Fire, both planned burns and wildfire, is a widespread and common occurrence in the Little Desert National Park resulting in very few remaining tracts of long-unburnt vegetation there. Previous work in similar habitat has shown leaf litter and canopy cover may take 20–40 years to return to pre-fire levels (Haslem et al. 2011). Nevertheless, overall vegetation structure was similar between fragment types (10 of 14 metrics were similar), vegetation type the same and time-since-fire matched as close as possible given the high frequency of fire in the region.

Does species richness and diversity differ between fragments and *pseudo*-fragments?

Species richness and diversity estimates were similar between paired fragments and pseudo-fragments. Thus, our results do not support the trend of reduced

Table 3 Model selection for generalised linear models exploring how fragment type and size influence individual species abundance (only models with delta AICc < 2 are shown)

Species	Model terms	df	QAICc	Delta QAICc	R^2
Lerista bougainvillii	Fragment type + size	3	52.8	0	0.753
	Fragment type + size + fragment type:size	4	53.5	0.70	0.804
Lampropholis delicata	Size	2	33.3	0	0.834
Ctenotus robustus	Fragment type + size + fragment type:size	4	36.7	0	0.999
	Fragment type	2	37.2	0.54	0.974
	Fragment type + size	3	37.5	0.83	0.993
Ctenotus orientalis	Size	2	39.8	0	0.922
Menetia greyii	Size	2	40.6	0	0.510
Christinus marmoratus	Size	2	38.1	0	0.745
	Fragment type + size	3	39.1	0.98	0.848
Amphibolurus norrisi	Fragment type + size	3	53.1	0	0.718
Morethia obscura	Size	2	36.4	0	0.992
Ctenophorus pictus	Null	1	29.9	0	0.000
	Size	2	31.4	1.41	0.316
Cercartetus lepidus	Fragment type + size + fragment type:size	4	54.6	0	0.928
Cercartetus concinnus	Null	1	36.4	0	0.000
	Size	2	37.8	1.37	0.184
Pseudomys apodemoides	Size	2	31.4	0	0.984
	Fragment type + size	3	31.6	0.23	0.999
Limnodynastes dumerilii	Fragment type + size	3	36.2	0	0.944
	Fragment type	2	37.9	1.66	0.787
Tiliqua rugosa	Fragment type	2	39.8	0	0.358
	Fragment type + size	3	41.7	1.9	0.381
Aprasia striolata	Fragment type + size	3	43.3	0	0.333
	Size	2	43.8	0.44	0.231
Neobatrachus sp.	Null	1	31.9	0	0.000
	Size	2	32.7	0.81	0.303
	Fragment type	2	33.8	1.87	0.148
Mus musculus	Fragment type + size	3	40.0	0	0.911
Pygopus lepidopodus	Fragment type + size	3	40.4	0	0.454
	Fragment type + size + fragment type:size	4	41.4	0.98	0.502

species richness in modified landscapes predicted by both the habitat amount hypothesis and island biogeography theory, and supported by several comprehensive meta-analyses (Newbold et al. 2015; Thompson et al. 2016; Cordier et al. 2021).

Declines in species richness after land modification are primarily driven by two processes. First, species are lost as habitat area decreases via the sample area effect (Fahrig 2013). Second, ecosystem decay alters the demography of remaining species in fragmented habitats over time, leading to increased extinction risk (Chase et al. 2020). Despite the negative effect of these processes, similar richness (Schutz and Driscoll 2008), and in some instances, higher richness in modified landscapes (Suazo-Ortuno et al. 2008) have been reported. Modified habitats, such as fragments, may offer additional resources (resource subsidies) for some taxa including increased food availability and altered thermoregulatory conditions (Nowakowski et al. 2018; Doherty et al. 2019), potentially increasing available niches and counterbalancing the negative effect on species richness of ecosystem decay.

Fragment size was an important predictor for species richness and diversity, with larger fragments

Table 4 Estimated model coefficients for generalised linear models exploring how fragment type and size influence individual species abundance (only models with delta AICc < 2 are shown). Significant effects (85%) are shown in bold

Species	Predictors	Estimate	CI (85%)
Lerista bougainvillii	(Intercept)	− 0.34	− 1.09 to 0.41
	Fragment type [Fragment]	1.44	**0.63–2.25**
	Size	0.56	**0.18–0.95**
	(Intercept)	− 0.21	− 0.88 to 0.46
	Fragment type [Fragment]	1.19	**0.40–1.98**
	Size	− 0.13	− 0.80 to 0.54
	Fragment type [Fragment] × size	0.92	**0.13–1.72**
Lampropholis delicata	(Intercept)	1.68	1.29–2.07
	Size	0.61	**0.20–1.02**
Ctenotus robustus	(Intercept)	− 0.41	− 2.69 to 1.86
	Fragment type [Fragment]	3.07	**0.75–5.38**
	Size	2.36	**0.35–4.37**
	Fragment type [Fragment] × size	− 2.15	**− 4.20** to **− 0.10**
	(Intercept)	1.24	0.16–2.32
	Fragment type [Fragment]	1.43	**0.23–2.64**
	(Intercept)	1.16	0.20–2.12
	Fragment type [Fragment]	1.43	**0.38–2.48**
	Size	0.42	− 0.06 to 0.90
Ctenotus orientalis	(Intercept)	2.01	1.71–2.30
	Size	0.62	**0.31–0.93**
Menetia greyii	(Intercept)	0.30	− 0.15 to 0.75
	Size	0.77	**0.30–1.24**
Christinus marmoratus	(Intercept)	1.63	1.29–1.97
	Size	0.55	**0.19–0.91**
	(Intercept)	1.89	1.48–2.30
	Fragment Type [Fragment]	− 0.61	− 1.25 to 0.02
	Size	0.55	**0.18–0.92**
Amphibolurus norrisi	(Intercept)	0.58	0.25–0.90
	Fragment type [Fragment]	− 2.44	**− 3.44** to **− 1.45**
	Size	0.61	**0.28–0.95**
Morethia obscura	(Intercept)	2.70	2.44–2.96
	Size	0.61	**0.33–0.88**
Ctenophorus pictus	(Intercept)	0.95	0.38–1.52
	(Intercept)	0.87	0.31–1.44
	Size	0.42	− 0.18 to 1.03
Cercartetus lepidus	(Intercept)	1.69	1.41–1.98
	Fragment type [Fragment]	− 2.74	**− 4.26** to **− 1.22**
	Size	0.27	− 0.03 to 0.58
	Fragment type [Fragment] × size	1.80	**0.42–3.18**
Cercartetus concinnus	(Intercept)	0.76	0.37–1.15
	(Intercept)	0.71	0.32–1.09
	Size	0.33	− 0.08 to 0.74
Pseudomys apodemoides	(Intercept)	1.75	1.02–2.49
	Size	0.89	**0.13–1.65**
	(Intercept)	2.18	1.41–2.94
	Fragment type [Fragment]	− 1.18	− 2.42 to 0.05
	Size	0.89	**0.16–1.62**

Table 4 (continued)

Species	Predictors	Estimate	CI (85%)
Limnodynastes dumerilii	(Intercept)	0.47	− 0.36 to 1.31
	Fragment type [Fragment]	1.30	**0.39–2.21**
	Size	0.63	**0.17–1.10**
	(Intercept)	0.65	− 0.33 to 1.63
	Fragment type [Fragment]	1.30	**0.19–2.40**
Tiliqua rugosa	(Intercept)	− 2.4	− 3.89 to − 0.90
	Fragment type [Fragment]	2.40	**0.83–3.96**
	(Intercept)	− 2.43	− 3.86 to − 1.01
	Fragment type [Fragment]	2.40	**0.92–3.88**
	Size	0.28	− 0.17 to 0.73
Aprasia striolata	(Intercept)	− 1.59	− 2.56 to − 0.63
	Fragment type [Fragment]	1.10	**0.08–2.12**
	Size	0.84	**0.24–1.45**
	(Intercept)	− 0.90	− 1.51 to − 0.29
	Size	0.84	**0.22–1.47**
Neobatrachus sp.	(Intercept)	0.46	− 0.15 to 1.08
	(Intercept)	0.34	− 0.34 to 1.01
	Size	0.54	− 0.18 to 1.25
Mus musculus	(Intercept)	− 2.64	− 4.61 to − 0.67
	Fragment type [Fragment]	2.48	**0.66–4.31**
	Size	1.65	**0.68–2.61**
Pygopus lepidopodus	(Intercept)	− 0.72	− 1.45 to 0.01
	Fragment type [Fragment]	− 1.5	− **2.64** to − **0.37**
	Size	1.16	**0.46–1.86**
	(Intercept)	− 0.55	− 1.20 to 0.10
	Fragment type [Fragment]	− 4.92	− 10.32 to 0.49
	Size	0.93	**0.27–1.60**
	Fragment type [Fragment] × size	3.25	− 1.10 to 7.59

having higher species richness and slightly higher diversity. This is congruent with both the sample area effect and island biogeography theory. Whilst a large fragment is predicted to hold higher richness than a small one, when comparing an equal amount of habitat between single large and several small fragments (SLOSS approach), island biogeography theory predicts lower richness in several small fragments, whereas the habitat amount hypothesis is "equally compatible with either outcome of SLOSS" (Fahrig 2021). Recent evidence contradicts the island biogeography theory, finding small fragments often outperform large ones (Wintle et al. 2019; Riva and Fahrig 2022). The mechanisms driving this pattern are not fully understood but may include: increased functional connectivity, spreading of extinction risk, and landscape complementation (Fahrig 2003). Our data showed no evidence of an island effect (Macarthur and Wilson 1967), where species area curves are steeper for fragments compared to pseudo-fragments, indicating small fragments studied here were not depauperate of herpetofauna and small mammal species studied, providing support for the high value of small fragments (Fahrig 2013). Additionally, two threatened species were only detected in fragments (*E. curta* and *S. crassicaudata*) compared to one threatened species only detected in pseudo-fragments (*V. rosenbergi*) suggesting fragments provide habitat for rare species as well as common ones.

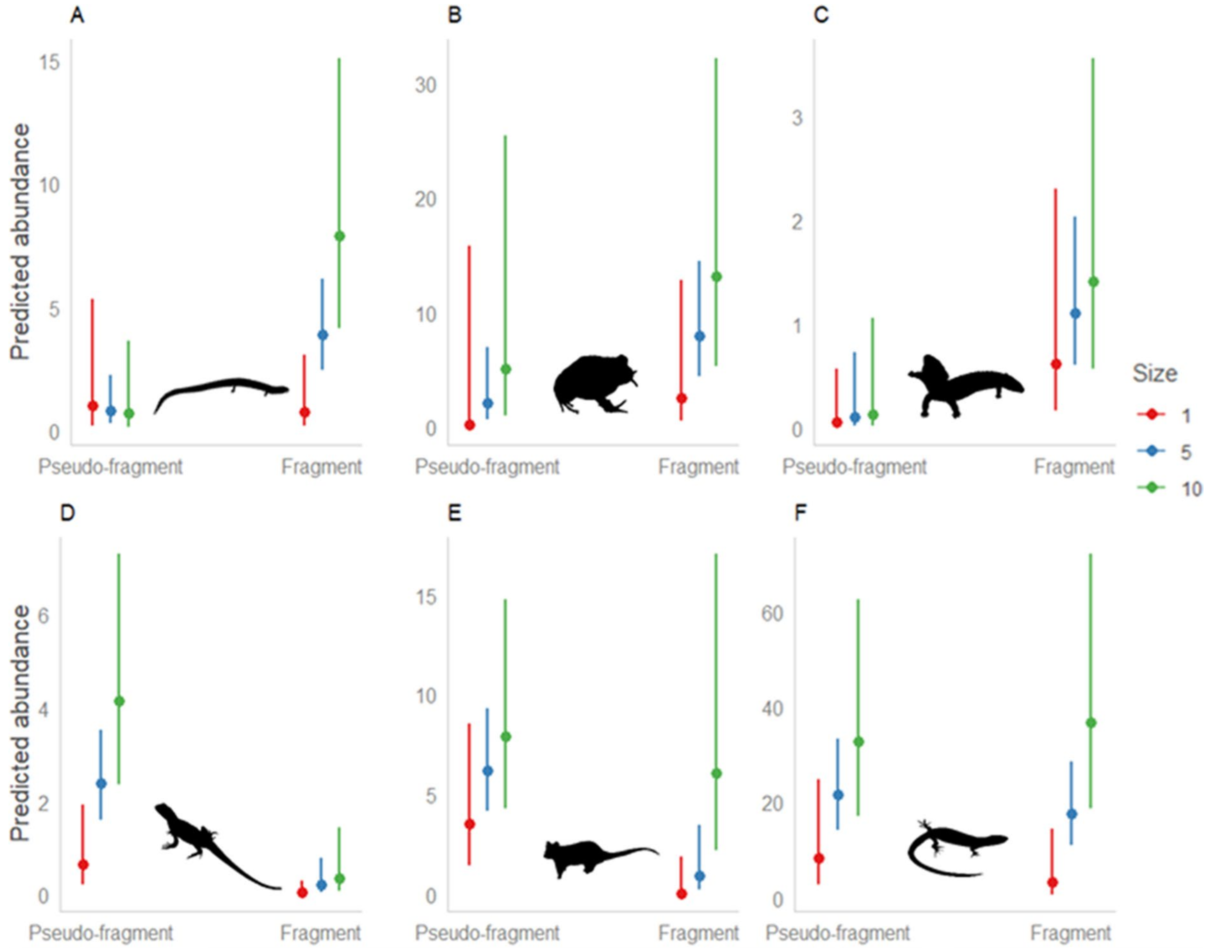

Fig. 6 Predicted abundances of: **A** *Lerista bougainvilli*, **B** *Limnodynastes dumerilii*, **C** *Tiliqua rugosa*, **D** *Amphibolurus norrisi*, **E** *Cercartetus lepidus*, **F** *Morethia obscura* in fragments and pseudo-fragments of sizes 1, 5 and 10 hectares. Plots are derived from the highest performing model for each species (Table 3). Plots **B**, **C** and **D** relate to additive models whilst the models for **A**, **E** and **F** contain an interaction term (Table 4)

Table 5 Model selection for multiple regression models exploring how traits influence species response to fragmentation (top five performing models shown)

Model terms	df	AICc	Delta AICc	R^2
Diet + habit + habitat breadth	7	38.2	0	0.799
Diet + habit	6	40.7	2.52	0.668
Habit + habitat breadth	5	41.5	3.37	0.533
Habit	4	41.9	3.70	0.393
Activity time + habitat breadth + temperature regulation	6	42.7	4.47	0.627

Does community composition differ between fragments and *pseudo*-fragments?

We found a significant difference in species composition between fragments and pseudo-fragments. Despite 22 of 26 species being detected in both fragment types, the ordination showed a clear separation between the community composition of fragments and pseudo-fragments. Similarly, Kay et al. (2018) found modified sites differed in composition but not richness, compared with intact sites. Therefore, remnant fragments can host novel communities (Morse et al. 2014), containing combinations of

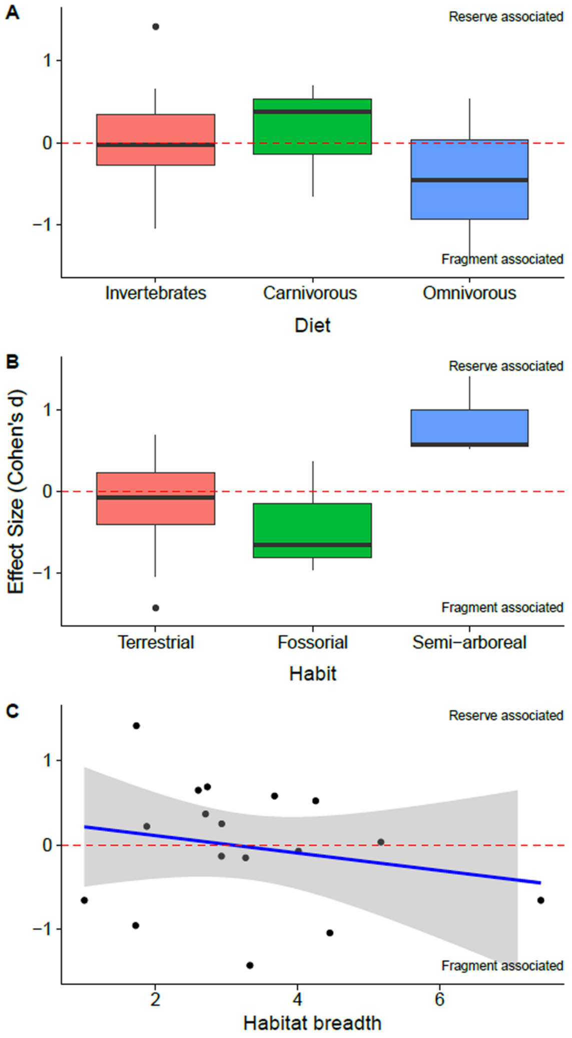

Fig. 7 Effect of species traits—diet (**A**), habit (**B**) and habitat breadth (**C**)—on abundance. Positive effect size indicates higher abundance in pseudo-fragments, negative effect size indicates higher abundance in fragments

Table 6 Estimated model coefficients from the only supported model (delta AICc < 2) showing the influence of species traits on effect size (Cohen's d)

Predictors	Estimate	85% CIs
Intercept	0.69	0.22 to 1.15
Diet (Carnivorous)	0.67	**0.31 to 1.02**
Diet (Omnivorous)	– 0.74	**– 1.32 to – 0.16**
Habit (Fossorial)	– 1.03	**– 1.47 to – 0.59**
Habit (Semi– arboreal)	1.17	**0.71 to 1.63**
Habitat breadth	– 0.22	**– 0.35 to – 0.10**

Positive values indicate higher abundance in pseudo-fragments whilst negative values indicate higher abundance in fragments

fauna species that did not co-occur in the study area prior to land modification.

One lizard (*A. norrisi*) and one marsupial (*C. lepidus*) were deemed 'indicator' species characteristic of pseudo-fragment species assemblages. Several characteristics of remnant fragments may lead to species decline and contraction toward continuous habitat. First, livestock grazing in fragments can reduce habitat quality, limiting food and shelter resources for some species (Driscoll 2004; Cordier et al. 2021). However, in some cases, grazing has shown negligible effects on fauna communities (Read 2002; Michael et al. 2018) indicating grazing context (i.e., stock density, grazing duration) may be important. Second, edge effects may have a negative effect on some species. For example, high edge:area ratio can result in more intense visitation by introduced predators and, thus, higher predation pressure on species vulnerable to such predators (Didham et al. 2007; Graham et al. 2012). Indeed, in our study, fox activity was significantly higher in fragments compared to pseudo-fragments. Third, fragment isolation can reduce immigration and emigration, interrupting population dynamics (Fischer and Lindenmayer 2007). Williams et al. (2012) found reptile species more likely to occur in a fragment when in close proximity to a large section of continuous habitat, implying dispersal is critical to 'rescue' or recolonise fragments. Both pseudo-fragment indicator species are arboreal, likely reducing their dispersal ability across the treeless agricultural matrix (Hansen et al. 2020), and contributing to their reduced abundance in fragments. Here, we see an 'island effect' where these species are most abundant on the 'mainland', in this case the continuous habitat of the reserve, and show reduced abundance as fragment size decreases.

Despite the widespread negative consequences of land modification, some native species are more abundant in modified landscapes. We identified five indicator species characteristic of fragments and consider several possible explanations for their higher abundance in fragments. First, agricultural landscapes may offer increased resources (Doherty et al. 2019) for species able to access them facilitating increased survival and reproductive success. For instance, farm dams and drainage lines inadvertently create breeding habitat for water-dependent species (Knutson et al. 2004) like the frog, *L. dumerilii*, which was abundant in fragments. Second, altered exposure to disturbances, such as fire, may increase habitat suitability for some species (Nimmo et al. 2012). The absence of fire in fragments may benefit species that prefer long-unburnt habitat (Haslem et al. 2011), like the leaf-litter-dwelling lizard, *L. bougainvilii,* which showed higher abundance in fragments. Indeed, vegetation surveys in our study showed that fragments had significantly deeper leaf litter, and more structural complexity at high and canopy strata, possibly a result of fire exclusion from fragments. Third, 'hard' fragment edges discourage emigration which can lead to a 'crowding' or 'concentration' effect (Grez et al. 2004; Tscharntke et al. 2012), increasing a species' population density. This effect is likely strongest for species with low dispersal ability, like the pygopodid, *A. striolata,* which had higher abundance in fragments. Importantly, factors driving a species' response can operate in tandem. For example, after fragmentation, *L. bougainvilli* might increase in number due to the concentration effect. Then, over time, leaf litter may accumulate in the absence of fire, and the cultivation of crops in the surrounding matrix cause a spillover of agricultural pest insects resulting in better habitat and more food resources for the skink, increasing the carrying capacity of the population in the fragment.

Do traits mediate species abundance in fragments and *pseudo*-fragments?

Ecological traits influence a species' response to fragmentation, where some species are better equipped to withstand disturbance compared to others (Henle et al. 2004; Keinath et al. 2017; Doherty et al. 2020). We found three traits—diet, habitat breadth and habit—affect species abundance between fragments and pseudo-fragments. An omnivorous diet provides a wider range of food items to exploit post-disturbance when food resources may be altered, whereas carnivorous species must continue to hunt prey animals to survive, even when prey numbers are reduced. Similarly, species with broad habitat requirements can find refuge in a variety of habitats compared to those with narrow habitat requirements which are reliant on a select few habitat types, making them vulnerable to extinction when these habitats are altered (Lettoof et al. 2023). These traits—diet and habitat breadth—are often assessed on a continuum of generalist to specialist. Our results support existing evidence that generalists are more abundant in fragmented agricultural landscapes compared to specialists which are more likely to be rare or locally extinct (Driscoll 2004; Michael et al. 2015; Keinath et al. 2017; Simpson et al. 2023).

Compared to terrestrial species, semi-arboreal species were more abundant in pseudo-fragments and fossorial species more abundant in fragments. It is possible that, for both groups, reduced dispersal influences species' responses but in opposite directions. After fragmentation, fossorial species may increase in density through a concentration effect where individuals are no longer dispersing due to hard fragment edges (Grez et al. 2004; Tscharntke et al. 2012). Fossorial species may be buffered from negative effects of fragmentation, such as grazing and increased predation by introduced predators, by their ability to take refuge underground. Additionally, fossorial species included in our study have small body size and home ranges meaning small fragments can support large populations. In contrast, the two semi-arboreal reptiles in our study are comparatively large-bodied with larger home ranges resulting in fewer individuals occupying an equivalent area. As arboreal species are presumably less likely to cross the treeless agricultural matrix, reduced immigration from nearby populations in large tracts of habitat may leave arboreal species vulnerable to decline in fragments (Hoehn et al. 2007; Munguia-Vega et al. 2013). On the other hand, one study found arboreality to increase resistance to land modification (Neilly et al. 2018), and the abundance of one semi-arboreal mammal species in our study, *Cercartetus concinnus*, was similar between fragments and pseudo-fragments. Further research is needed to disentangle the relative effects of traits driving species' responses to fragmentation.

Conservation implications

We show that fragments can contain novel communities, including threatened species, not present in continuous habitat. These distinct communities are shaped by traits advantageous to survival in altered landscapes and may provide an important source of adaptability to maintain ecosystem function in the face of continued human disturbance. Furthermore, fragments may provide 'insurance populations', safeguarded against large disturbances like wildfire and disease which have the capacity to spread through continuous habitat, decimating populations. Thus, small fragments may be highly complementary to large conservation reserves, and we support the growing body of evidence emphasising the importance of preserving small habitat patches.

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Author contributions Project conception (DMW, DGN, DMW, TSJ, CJJ, BH, DRM, EGR, WLG, AB, EL), data collection (DMW, GDL, CJJ, AA, DGN), analysis (DMW, DGN), writing, review and editing (all).

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Data availability Data will be publicly available from the Dryad digital repository.

Declarations

Competing interests The authors declare no conflict of interest.

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