ECOGRAPHY

Research

Generalist predator's niche shifts reveal ecosystem changes in an experimentally fragmented landscape

Julian Resasco, Kika T. Tuff, Saul A. Cunningham, Brett A. Melbourne, Andrew L. Hicks, Seth D. Newsome and Kendi F. Davies

J. Resasco (http://orcid.org/0000-0003-1605-3038) (jresasco@colorado.edu), K. T. Tuff, B. A. Melbourne (http://orcid.org/0000-0002-8843-4131), A. L. Hicks and K. F. Davies (http://orcid.org/0000-0001-7716-3359), Dept of Ecology and Evolutionary Biology, Univ. of Colorado at Boulder, Boulder, CO, USA. – S. A. Cunningham, Australian National Univ., Fenner School of Environment and Society, Canberra, Australia, and CSIRO Land and Water, Canberra, Australia. – S. D. Newsome, Dept of Biology, Univ. of New Mexico, Albuquerque, NM, USA.

Ecography
41: 1209–1219, 2018
doi: 10.1111/ecog.03476

Subject Editor: Miguel Matias
Editor-in-Chief: Miguel Araújo
Accepted 30 September 2017

Habitat fragmentation can alter the trophic structure of communities and environmental conditions, thus driving changes in biodiversity and ecosystem functions. Quantifying niches of generalist predators can reveal how fragmentation alters ecosystems. In a habitat fragmentation experiment, we used stable isotopes of a generalist predator skink to test predictions from spatial theory on trophic structure and to quantify abiotic changes associated with fragmentation among continuous forest, fragments, and matrix habitats. We predicted that in fragments and the matrix, isotopic niches would shift due to decreases in skink trophic positions ($\delta^{15}N$) from reductions in trophic structure of arthropod food webs and abiotic changes over time ($\delta^{13}C$) relative to continuous forest. Contrary to theoretical predictions, we did not find evidence of reductions in trophic structure with fragmentation. In fact, skink $\delta^{15}N$ values were higher in the matrix and fragments than continuous forest, likely due to changes in distributions of a detritivorous prey species. In addition, $\delta^{13}C$ values in the matrix decreased over years since fragmentation due to abiotic changes associated with matrix tree maturation. We show how isotopic niches are influenced by fragmentation via shifts in biotic and abiotic processes. The potential for either or both spatial and abiotic effects of fragmentation present a challenge for theory to better predict ecological changes in fragmented landscapes.

Introduction

As human pressure for resources intensifies, the proportion of land allocated to meeting those demands grows (Foley et al. 2007, 2011). This modification has come at a high cost to natural ecosystems (Hoekstra et al. 2005). While habitat conversion and fragmentation are major drivers of biodiversity loss (Vitousek et al. 1997, Wilcove et al. 1998, Sala et al. 2000, Pereira et al. 2010, Haddad et al. 2015), ecosystems, communities, and populations respond to fragmentation of their habitat

NORDIC SOCIETY OIKOS

www.ecography.org

in diverse ways, challenging ecologists to find the best approaches to quantify and synthesize these responses to better understand impacts of fragmentation.

The niche concept is useful for understanding and testing ecological responses to environmental stressors like habitat conversion and fragmentation (Holt 2009). Hutchinson (1957) formalized the ecological niche as an n-dimensional hypervolume whose axes represent the environmental and resource requirements of a species. According to Hutchinson (1978), scenopoetic axes represent the environmental conditions where an organism lives, while bionomic axes represent the trophic component of the niche space. Fragmentation can affect both scenopoetic and bionomic axes of a species' niche space due to known abiotic and biotic effects respectively (Saunders et al. 1991). However, a major challenge for disentangling the diverse effects of fragmentation on species and communities is how to quantify changes in niche axes (Fischer and Lindenmayer 2006, Layman et al. 2007a).

Niche axes are difficult to measure because of the quantity of data required and the challenge of determining what biotic and abiotic components are most relevant to adequately describe the niche of a given species (Chase and Leibold 2003, Newsome et al. 2007). In regards to biotic components, trophic interactions are often complex, cryptic, and dynamic and thus difficult to resolve directly (Morales-Castilla et al. 2015). In regards to abiotic components, while abiotic conditions of habitats can often easily be measured directly, interpreting these data as they relate to an organism's occurrence, abundance, and ecological role is difficult. The stable isotope composition of an organism can reflect both biotic and abiotic aspects of its niche (Bearhop et al. 2004, Newsome et al. 2007, Jackson et al. 2011), and can be used to quantify niche shifts that result from fragmentation (Layman et al. 2007b, Resasco et al. 2012) and other environmental stressors (Gibb and Cunningham 2011).

Nitrogen stable isotopes ($\delta^{15}N$) are often used to estimate trophic position (Gannes et al. 1998, Post 2002), which is a tractable component of the bionomic axis (Bearhop et al. 2004, Layman et al. 2007a, Newsome et al. 2007, Schmidt et al. 2007), because $\delta^{15}N$ is enriched in consumer tissues relative to that of prey by about 3–5‰ per trophic step (Vanderklift and Ponsard 2003). Among individuals or populations of a given species, $\delta^{15}N$ values can be used to detect changes in relative trophic position from subtle changes in food webs or diet shifts (Vander Zanden et al. 1999). On the other hand, carbon stable isotopes ($\delta^{13}C$) are commonly used to distinguish among relative contributions of different plant functional groups (e.g. C_3 and C_4) or to detect changes in the environment caused by variation in abiotic conditions like temperature and moisture (DeNiro and Epstein 1978, Hobson and Clark 1992, Ehleringer et al. 1993, Aranda et al. 2007, Newsome et al. 2007). These changes have important implications for ecosystem functions including productivity, decomposition, and water and nutrient cycling (Chapin et al. 1997, Petchey et al. 1999). When used in combination, the bivariate area defined by $\delta^{13}C$ and $\delta^{15}N$ values of individuals in an area reflect that populations' niche, the isotopic niche, because the isotopic composition of each individual is determined by resources it consumes and the habitat in which it lives (Newsome et al. 2007). Thus, we can use shifts in isotope values of generalist predators to synthesize the ecological effects of both biotic and abiotic changes that are driven by fragmentation.

How might habitat fragmentation affect a species' isotopic niche? In the case of $\delta^{15}N$, metacommunity theory predicts that fragmentation can alter the trophic structure of food webs by making species of higher trophic levels more susceptible to loss due to sequential dependencies on species of lower trophic levels ('donor-controlled model', Holt 1993, 1997, Holt and Hoopes 2005). Such loss of predators can result in 'trophic downgrading' in habitat fragments (Estes et al. 2011) and disrupt ecosystem stability (McCann 2000, Terborgh et al. 2001, Terborgh and Estes 2010). However, the effect of fragmentation on the trophic structure of communities can be complex (Holt and Hoopes 2005). Empirical evidence from systems surrounded by an inhospitable matrix (e.g. lakes, islands) support theory that habitat area and connectivity are inversely related to food chain length and predator persistence (Schoener 1989, Vander Zanden et al. 1999, Post et al. 2000, Terborgh et al. 2001, Takimoto et al. 2008). There is also evidence that species within the same trophic level respond to environmental gradients among lakes in similar ways (Matias et al. 2017). However, while there is evidence for the same in fragmented forest systems (Davies et al. 2000, Komonen et al. 2000), the trophic effects of fragmentation and the mechanisms at work are often unclear (Henle et al. 2004, Ryall and Fahrig 2006, Martinson and Fagan 2014). This ambiguity may be in part because of variation in hospitability of the matrix (Brudvig et al. 2017) and because fragmentation causes changes in the abiotic environment such as altered temperature, wind, and water (Saunders et al. 1991, Haddad et al. 2015, Tuff et al. 2016, Resasco et al. 2017a) that affect ecosystem functioning and can differentially affect the distribution and abundance of species at different trophic levels. These considerations are not usually included in fragmentation theory (Harrison and Bruna 1999).

Adding to the uncertainty of fragmentation effects is the nuisance of confounding factors, such as disturbance and non-random conversion of habitat – all of which tend to accompany fragmentation (Ewers and Didham 2006). Controlled experiments provide a solution to this problem because they allow for the control of extraneous variables (Debinski and Holt 2000, Collinge 2009) but implementing such experiments with replication and at scales comparable to management activities is difficult. Consequently only a few such experiments exist worldwide (Debinski and Holt 2000, Haddad et al. 2015).

The Wog Wog Habitat fragmentation experiment (henceforth Wog Wog) in southeastern Australia is replicated, controlled, randomized, large-scale, and long-term (Fig. 1). Also, because it contains sites of continuous natural habitat

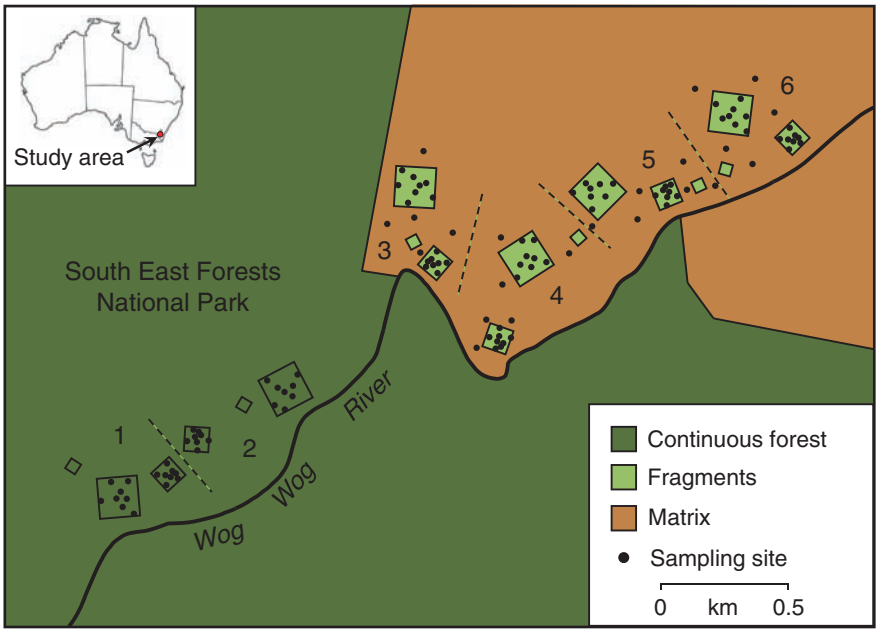

Figure 1. Diagram of the Wog Wog habitat fragmentation experiment. Dark green colored areas represent native continuous eucalypt forest, light green colored areas represent eucalypt fragments, and bronze colored areas represent a pine plantation monoculture. Four remnant blocks (each with three size treatments: 0.25, 0.875, and 3.062 ha) are embedded in the pine plantation matrix and two control blocks are embedded in continuous eucalypt forest. There are eight monitoring sites (represented by dots) within each patch, each with two pitfall traps. Dots in the pine matrix between the fragments represent the location of a pair of monitoring sites (a slope site and a drainage-line site) established after fragmentation. Eight monitoring sites on each small fragment are not shown because of space constraints.

and fragments of multiple sizes, results are widely applicable to management of fragmented ecosystems. In this study, we asked if eucalypt forest fragmentation and conversion to a pine plantation monoculture altered the niche of an abundant generalist predator, the pale-flecked garden sunskink *Lampropholis guichenoti* (henceforth skink), using almost a decade of post-fragmentation data. Generalist predators often persist in fragments (Layman et al. 2007b , Gravel et al. 2011), and because they consume prey in proportion to its availability, their diet can be used to detect fragmentation-driven changes in ecosystems to trophic structure and the abiotic environment.

Specifically, we asked whether experimental eucalypt forest conversion and fragmentation resulted in 1) decreases in the trophic position of skinks, 2) simultaneous changes in its abiotic environment that would be reflected in skink $\delta^{13}C$ values, and 3) overall changes of the isotopic niche of this generalist predator. Because fragmentation is predicted to cause declines in potential prey of higher trophic rank we predicted that forest conversion and fragmentation would reduce the trophic position of skinks (prediction for 1). Next, we predicted that changes in abiotic conditions associated with pine matrix maturation would result in decreases in skink $\delta^{13}C$ values in the matrix, driven by decreases in $\delta^{13}C$ values in understory plants (prediction for 2). Because nearly all plants at Wog Wog use the C_3 photosynthetic pathway (Austin and Nicholls 1988), we did not predict $\delta^{13}C$ would change in response to C_3 versus C_4 plant availability. We also expected to find that skinks in fragment edges would have intermediate $\delta^{15}N$ and $\delta^{13}C$ values between those of the matrix and fragment interiors. Lastly, we predicted that the shifts in $\delta^{15}N$ and $\delta^{13}C$ would change the location and size of the isotopic niche (prediction for 3).

Methods

Study system

Eucalypt forests are the dominant forest type in Australia and are characterized by a canopy of *Eucalyptus* and confamilials. Large areas of eucalypt forests have been cleared, leaving fragmented remnant forests (Hobbs 2001, National Forest Inventory 2013), resulting in the disruption of ecosystem processes (Hobbs 1993). Eastern Australia is listed as a 'global deforestation front' by the World Wildlife Fund, although recent legislation has protected forests in New South Wales (Taylor 2015).

The Wog Wog experiment is located in New South Wales, Australia (37°04′30″S, 149°28′00″E; Fig. 1) and consists of eucalypt forest fragments of three sizes of 3.5 fold increments: 0.25 ha (small), 0.88 ha (medium), and 3.06 ha (large) fragments, within four replicate blocks (12 fragments total; Fig. 1). These fragments were preserved when the surrounding land was cleared for a Monterey pine *Pinus radiata* plantation (matrix) in 1987–1988. Two blocks of the same layout are delineated within an adjacent continuous eucalypt

forest (Fig 1); Margules (1992) provides further description of the experimental design and sampling methods.

At Wog Wog, monitoring for ground-dwelling invertebrates was done using pitfall traps at sampling sites between 1985 (two years prior to fragmentation) to 1999. Each sampling site consisted of paired pitfall traps (5–10 m apart), which were constructed by placing a 90 mm-diameter cup into a PVC sleeve set permanently in the ground, flush with the surface. A drift fence embedded in the ground and abutting the rim of the cup extended 0.6 m and increased capture rate by directing ground-dwelling organisms into the trap. A 20-cm roof positioned over the trap protected the trap from flooding. Skink individuals were collected as accidental bycatch in pitfall traps during this sampling period and stored in 75:25% ethanol:water solution at the CSIRO Australian National Wildlife Collection. Ethanol preservation has been shown to affect stable isotope values in various taxa and tissues, especially for $\delta^{13}C$ (Sarakinos et al. 2002, Bugoni et al. 2008, Krab et al. 2012). However, Hobson et al. (1997) showed that ethanol preservation does not have a significant effect on muscle tissue $\delta^{13}C$ and $\delta^{15}N$ values. Moreover, because all samples were stored identically, were lipid extracted, and were all stored in ethanol solution for decades it is unlikely that preservation would bias experimental contrasts. Within each fragment or delineated 'fragment' within the continuous eucalypt forest, there were eight sampling sites, which were stratified in two ways: 1) by topography into slopes and drainage lines because the vegetation communities associated with these topographic features were different, and 2) by proximity to the fragment edge (edge and interior sites). There were two monitoring sites in each of the four strata (slope edge, slope interior, drainage-line edge, drainage-line interior), totaling eight sites within each fragment and a total of 144 sites over the 18 fragments and control sites. In the matrix there were 44 additional sampling sites between fragments (Fig. 1).

The skink *Lampropholis guichenoti* is widespread in eastern Australia. It is characterized as a generalist consumer of invertebrates (Lunney et al. 1989) and a habitat generalist (Lunney et al. 1989, Wilson 2012). At Wog Wog, they were common in all sampled habitats (continuous eucalypt forest, eucalypt fragments, and matrix) during the focal sampling period (Tuff 2016). They maintain relatively small home ranges of < 20 m^2 (Anderson and Burgin 2002), which are suited to the spatial scale of the experiment.

Tissue collection and stable isotope analysis

We collected liver, muscle (from base of tail), and gut (foregut, hindgut, and stomach) samples from 182 museum specimens of skinks that were selected to represent nearly all 188 sampling sites (Supplementary material Appendix 1 Table A1) from 1988–1997, 2–12 yr post fragmentation (overall mean $\pm$ SD of years since fragmentation = 6.9 $\pm$ 2.5; by treatment: continuous forest = 6.9 $\pm$ 2.4, fragments = 7.2 $\pm$ 2.7, and matrix = 6.3 $\pm$ 2.2; ANOVA: $F_{2,179} = 1.38$, $p = 0.25$). We stored skink tissues in a 75:25% ethanol:water solution. We removed prey items from the gut and identified them to the finest taxonomic resolution feasible, most frequently to the level of order. We measured $\delta^{13}C$ and $\delta^{15}N$ in both liver and muscle because these tissues differ in isotopic incorporation rate; liver turns over faster than muscle (e.g. $\delta^{13}C$ half-life in prairie lizard *Sceloporus undulatus* liver and muscle tissue is 14.8 and 56.1 d respectively; Warne et al. 2010, Vander Zanden et al. 2015). However, because results for both tissues were similar and did not change our interpretation we only report isotope data for muscle tissue in the main text. For data from both muscle and liver see Data deposition and Supplementary material Appendix 1. We also analyzed common skink prey that were collected in pitfall traps to help interpret how isotopic shifts in skinks related to trophic position (Supplementary material Appendix 1 Table A3).

Because variation in lipid content among individuals can bias $\delta^{13}C$ values (Post et al. 2007) we lipid-extracted skink liver and muscle samples using three sequential soaks in 2:1 chloroform:methanol solvent solution over a 72-h period, followed by repeated rinses in deionized water. We then freeze-dried samples and weighed 0.5–0.6 mg of sub-sample into a tin capsule. $\delta^{13}C$ and $\delta^{15}N$ values were measured using a Costech 4010 or CarloErba NC2500 elemental analyzer interfaced with a Thermo Scientific Delta V mass spectrometer at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM). Isotopic results are expressed as δ values, where $\delta^{13}C$ or $\delta^{15}N = [(R_{sample} - R_{standard}) - 1] \times 1000$, where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ of the sample and standard, respectively. The internationally accepted standards for $\delta^{13}C$ and $\delta^{15}N$ values are Vienna Pee Dee Belemnite (V-PDB) and atmospheric nitrogen, respectively. Values are expressed as per mil (‰). Precision for $\delta^{13}C$ and $\delta^{15}N$ was estimated by analysis of internal protein reference materials; within and among run variation (SD) was $\leq$ 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$. We also analyzed the weight percent carbon and nitrogen concentrations of each sample, which are reported as [C]/[N] (Supplementary material Appendix 1 Table A2).

Experimental design and data analysis

The Wog Wog experiment has a hierarchical structure with fixed and random effects at three spatial scales. Individuals were trapped at pitfall trap *Sites*, which are nested within *Plots* (fragments or delineations of the same dimensions within the continuous eucalypt forest), which are nested within *Replicates* (Fig. 1). We included two random effects: *Replicate and Plot*. Five fixed effects were included in models as follows. 1) *Fragmentation treatment*: a categorical variable with two levels, (1) eucalypt forest fragments and (2) continuous eucalypt forest. In separate models we also examined a categorical variable, *Fragmentation treatment and matrix*, with three levels, (1) forest fragments, (2) continuous forest, and (3) pine plantation matrix. 2) *Fragment size*: a categorical variable that

describes the interaction between fragmentation and size. It has four levels: (1) small, (2) medium, (3) large, and (4) continuous forest, and tests for an effect of plot size nested within the fragmentation treatment. 3) *Edge*: a variable that describes the interaction between fragmentation and edges. It has three levels: (1) edge, (2) interior, and (3) continuous forest. 4) *Topography*: a categorical variable nested within plots with two levels, (1) slope, and (2) drainage lines. 5) *Fragment size edge*: a categorical variable representing the three way interaction with seven levels, (1) small edge, (2) small interior, (3) medium edge, (4) medium interior, (5) large edge, (6) large interior, and (7) continuous forest. We compared changes in deviance between nested linear mixed models to test the effects of the variables above on $\delta^{13}C$ and $\delta^{15}N$ values. We used a linear mixed model for both $\delta^{13}C$ and $\delta^{15}N$ since residuals were normally distributed. We fit models using the R package lme4, ver. 1.1-7 (Bates et al. 2015). To explore the effect of pine matrix maturation over time on $\delta^{13}C$ and $\delta^{15}N$ values we examined the effect of time (*Year*) and the interaction of *Year* × *Fragmentation treatment and matrix*. Because intraspecific density can affect the trophic ecology of individuals (Evangelista et al. 2014), we tested for an effect of skink density (the number of skinks in a pitfall trap corresponding to a given sampled skink) on $\delta^{13}C$ and $\delta^{15}N$ values using nested linear mixed models like those described above. We also examined the relationship between body size and $\delta^{13}C$ and $\delta^{15}N$ values for a subset of 149 individuals (82% of all individuals) for which we had data on snout–vent length (SVL; Tuff 2016) using linear regression.

To address whether habitat conversion and fragmentation caused shifts and reductions in isotopic niches, we quantified isotopic niches by calculating $\delta^{13}C$ vs $\delta^{15}N$ standard ellipse areas corrected for sample size, SEA_C, using the R package Stable Isotope Bayesian Ellipses in R, 'SIBER' ver. 2.1.3 (Jackson et al. 2011). This metric is robust to sample size differences at sample sizes of approximately ten or greater. We tested for isotopic niche differentiation using a permutation test that compared the observed area of overlap for pairwise combinations of ellipses to those from 10 000 permuted ellipses where labels were randomized. We tested for differences in isotopic niche area between treatments by drawing 10 000 bootstrapped samples (with replacement) and calculating ellipse areas to generate 95% CIs and test for pairwise differences. We also tested for differences at three time intervals (2–5, 6–7, and 8–11 yr) post fragmentation. Time intervals were chosen to return at least nine data points per treatment.

To assess the potential for baseline shifts among treatments, that is differences in $\delta^{13}C$ and $\delta^{15}N$ values throughout food webs, we analyzed 130 individuals of a primary consumer species, a cryptorhynchine weevil (family: Curculionidae, tribe: Cryptorhynchini) that is common across treatments. Cryptorhynchine weevils are xylophagous and typically feed on dead wood and bark, which are important basal sources for forest food webs.

To determine the effect of habitat conversion and fragmentation on prey we calculated the probability of occurrence of invertebrate orders found in skink guts among the continuous forest, fragments, and matrix. We analyzed the seven most common prey orders that were present in more than six individuals. We used generalized linear mixed models specifying a binomial distribution and *Replicate* as a random effect. We estimated effect sizes as the log odds ratio and calculated confidence intervals based on profile likelihoods. We used the R package lme4, ver. 1.1-7 (Bates et al. 2015). For one order, Amphipoda, we fit models using brglm (bias-reduced GLMs) ver. 0.5.9 (Kosmidis 2013) because of separation of the response variable among treatments; amphipods were absent in the guts of skinks collected in the matrix. We tested for differences in prey order richness among treatments using sample-based rarefaction and resulting 95% confidence intervals for equivalent numbers of skink individuals (samples) using the R package vegan, ver. 2.2-1 (Oksanen et al. 2010). For all analyses we used R ver. 3.1.2 (R Core Team).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.56b81> (Resasco et al. 2017b).

Results

Skinks had higher $\delta^{15}N$ values in fragments by, on average, 0.7‰ compared to continuous forests (Fig. 2, Table 1, *Fragmentation treatment*, $p = 0.004$). Skink $\delta^{15}N$ values

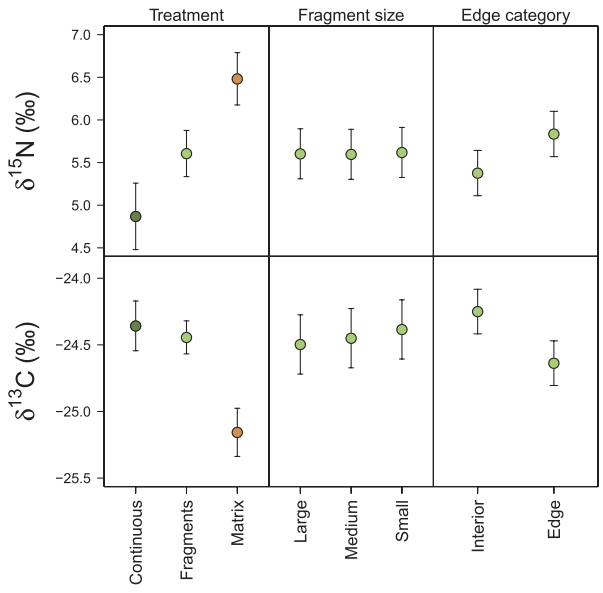

Figure 2. Model estimates and 95% CIs of skink (*Lampropholis guichenoti*) muscle $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) values for treatments within the fragmentation experiment. Colors represent habitat treatments, dark green: continuous eucalypt forest, light green: eucalypt fragments, bronze: matrix. Sample sizes for habitat treatments are: continuous eucalypt forest n = 42, eucalypt fragments n = 96, and matrix n = 44.

Table 1. Summary of the linear mixed model analyses of the effects of habitat fragmentation on skink (*Lampropholis guichenoti*) muscle $\delta^{13}C$ and $\delta^{15}N$ values. The significance of a variable was determined by the change in deviance (χ^2 statistic) between nested models associated with adding that variable. Line delineates analyses that include (above) and exclude (below) data from the matrix.

	Variables	df	χ^2	p-value
$\delta^{15}N$	*Fragmentation treatment and matrix*	2	41.45	$\mathbf{9.97 \times 10^{-10}}$
	Year	1	0.44	0.51
	Year × Fragmentation treatment and matrix	2	0.34	0.84
	Fragmentation treatment	1	8.20	**0.004**
	Fragment size	2	0.02	0.99
	Edge	1	15.78	$\mathbf{7.12 \times 10^{-5}}$
	Topography	1	0.01	0.93
	Fragment size + Edge	2	0.03	0.98
	Fragment size edge	2	3.02	0.22
$\delta^{13}C$	*Fragmentation treatment and matrix*	2	32.5	$\mathbf{8.59 \times 10^{-6}}$
	Year	1	12.5	**0.0004**
	Year × Fragmentation treatment and matrix	2	13.4	**0.001**
	Fragmentation treatment	1	0.62	0.43
	Fragment size	2	0.58	0.75
	Edge	1	10.6	**0.001**
	Topography	1	0.63	0.43
	Fragment size + Edge	2	0.63	0.73
	Fragment size × Edge	2	4.06	0.13

were 0.9‰ and 1.6‰ higher in the matrix relative to those collected in fragments and continuous forest respectively (Table 1, Fig. 2, *Fragmentation treatment and matrix*, $p < 0.001$). *Fragment size* had no effect on $\delta^{15}N$ values (Fig. 2, Table 1, *Fragment size*, $p = 0.99$). Within fragments, $\delta^{15}N$ values at fragment edges were intermediate between those of the matrix and fragment interiors and higher by, on average, 0.4‰ at edges compared to fragment interiors (Fig. 2, Table 1, *Edge*, $p < 0.001$). There was not a significant effect of topography nor fragment size-edge interaction on $\delta^{15}N$ values (Table 1, *Topography*, $p = 0.93$; *Fragment size edge*, $p = 0.22$). There was not a significant relationship between $\delta^{15}N$ and time since fragmentation (*Year*) overall (Table 1; $p = 0.51$) nor as an interaction with *Fragmentation treatment and matrix* (Supplementary material Appendix 1 Fig. A1, Table 1; $p = 0.84$). There was no relationship between SVL and $\delta^{15}N$ (slope = 0.01, $p = 0.60$, $r^2 = 0.002$).

There was not a significant difference in $\delta^{13}C$ values between fragments and continuous forest (Fig. 2, Table 1, *Fragmentation treatment*, $p = 0.43$). $\delta^{13}C$ values of skinks in the matrix were lower, on average, by 0.7‰ compared to fragments and 0.8‰ compared to continuous forest (Fig. 2, Table 1, *Fragmentation treatment and matrix*, $p < 0.001$). Fragment size did not have a significant effect on $\delta^{13}C$ values (Fig. 2, Table 1, *Fragment size*, $p = 0.75$). Within fragments, $\delta^{13}C$ values at fragment edges were intermediate between those of the matrix and fragment interiors and lower by an average of 0.4‰ at edges compared to fragment interiors (Fig. 2, Table 1, *Edge*, $p = 0.001$). There was not a significant effect of topography nor a fragment size by edge interaction on $\delta^{13}C$ values (Table 1, *Topography*, $p = 0.43$; Fragment size edge, $p = 0.14$). There was a significant effect of Year (Table 1, $p = 0.0004$) and an interaction of *Year* and *Fragmentation treatment and matrix* (Table 1, $p = 0.001$) on $\delta^{13}C$ values. There was a negative relationship between $\delta^{13}C$ and year in the matrix (slope = –0.19) that was weaker in fragments (slope = –0.044) and continuous forest (slope = –0.015; Supplementary material Appendix 1 Fig. A1).

Density of skinks in pitfall traps did not significantly affect $\delta^{15}N$ ($df = 1$, $\chi^2 = 1.12$, $p = 0.29$) or $\delta^{13}C$ values ($df = 1$, $\chi^2 = 1.39$, $p = 0.24$). However most of the sampled skinks (74%) had only a single skink present. Cryptorhynchine weevils did not significantly differ in $\delta^{13}C$ ($df = 2$, $\chi^2 = 0.34$, $p = 0.84$) or $\delta^{15}N$ ($df = 2$, $\chi^2 = 0.46$, $p = 0.79$) values among treatments. There was no relationship between SVL and $\delta^{13}C$ (slope = 0.02, $p = 0.31$, $r^2 = 0.01$).

Ellipses were significantly separated among treatments. Observed overlap among ellipses was smaller than expected by chance; overlap of ellipses (continuous vs fragments = 0.2‰^{2}, continuous vs matrix = 0‰^{2}, fragments vs matrix = 0.2‰^{2}) was much smaller than that of ellipses for randomly permuted data (all $p < 0.001$). Ellipse areas (SEA_C) were smallest in continuous forest (0.7‰^{2}), approximately two times larger in fragments (1.3‰^{2}), and approximately three times larger in the matrix (1.8‰^{2}; Fig. 3; all $p < 0.001$). However, these differences were not consistently seen within time intervals (Supplementary material Appendix 1 Fig. A1).

Of the 182 skink specimens we examined, 124 (68%) had identifiable gut contents. Parasitic nematodes were present (Jones and Resasco 2016) but were not considered prey and not included in our analysis. Prey items were identified to 16 invertebrate orders. Fragmentation and habitat conversion greatly reduced the probability of occurrence of terrestrial amphipods (*Arcitalitrus sylvaticus*) in skink stomach contents in fragments and the matrix but did not significantly

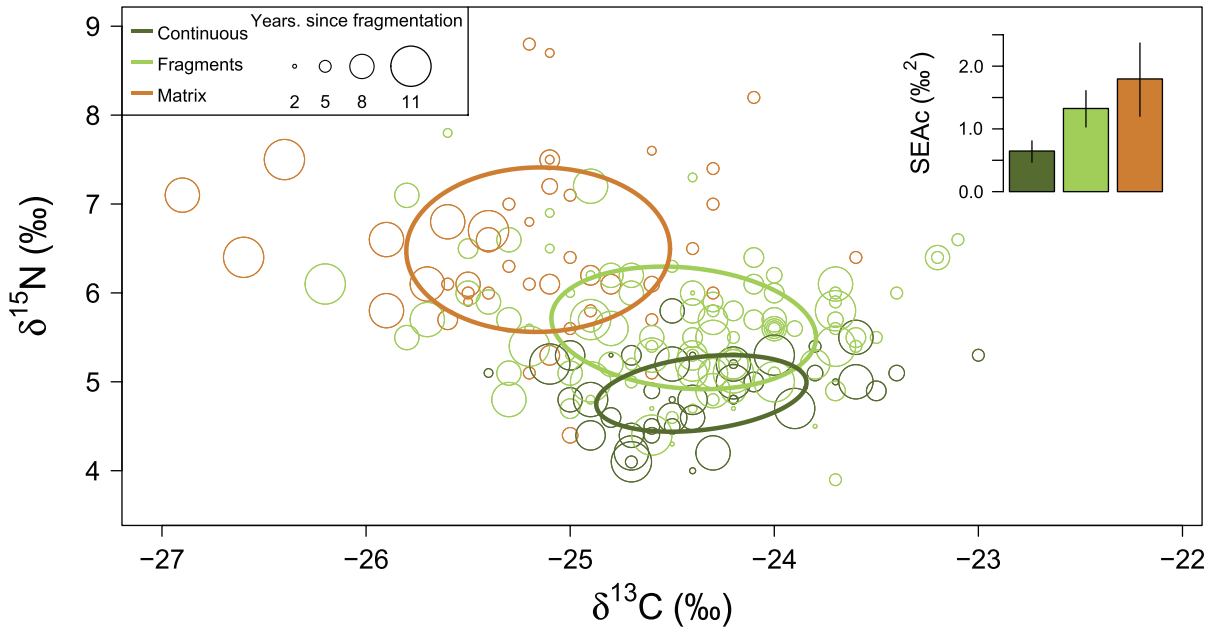

Figure 3. Bivariate plot of skink (*Lampropholis guichenoti*) muscle $\delta^{13}C$ and $\delta^{15}N$ values. Colors represent habitat treatments, dark green: continuous eucalypt forest, light green: eucalypt fragments, bronze: matrix. Circle sizes represent time in years since fragmentation. Thick solid lines represent sample size corrected standard ellipses (SEAc). Inset bar plot shows area in ‰^{2} of SEAc for each treatment with bootstrapped 95% CIs.

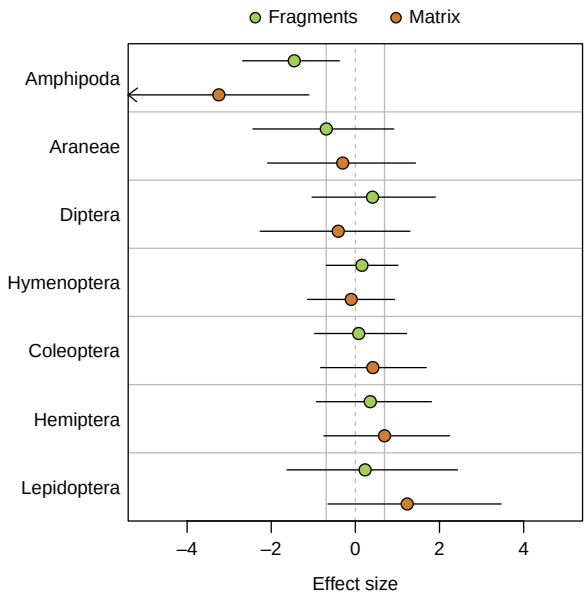

Figure 4. Effect sizes and 95% confidence intervals for the probability of occurrence of invertebrate prey orders found in guts of skinks (*Lampropholis guichenoti*) in response to habitat conversion and fragmentation. Effect sizes were calculated as the log odds ratio between fragments (light green circles) or matrix (bronze circles) and continuous forest. Vertical gray lines represent either a doubling (right of center) or halving (left of center) in the odds of occurrence. Arrow on confidence interval for amphipods indicates that interval extends to negative infinity due to complete separation among treatments due to absences of amphipods in skinks from the matrix.

affect other prey orders (Fig. 4). In the continuous forest, amphipods were common prey of skinks, however, they were much more uncommon in fragments and completely absent from skink guts in the matrix. Differences in prey trophic level were reflected in their $\delta^{15}N$ values. Ants and spiders, which were the most common prey according to gut content analysis, had $\delta^{15}N$ values that were 3.5 to 4.7‰ higher than amphipods (Supplementary material Appendix 1 Table A3). Prey order richness did not differ significantly among samples (rarified to 26 samples) from continuous forest (mean = 9.56, 95% CI: 8.41 to 10.69), fragments (mean = 10.57, 95% CI: 7.92 to 13.21), and matrix (mean = 8.93, 95% CI: 8.41 to 9.45).

Discussion

Habitat conversion and fragmentation resulted in both biotic and abiotic shifts in the niche of a generalist predator manifest as shifts in $\delta^{15}N$ and $\delta^{13}C$ values of skinks with habitat conversion and fragmentation. Shifts in $\delta^{15}N$ values were most likely attributable to changes in the trophic structure of the arthropod community consumed by skinks. Intriguingly, the direction of the shifts in $\delta^{15}N$ values associated with habitat conversion and fragmentation were opposite to our predictions based on theory. Shifts in $\delta^{13}C$ values were most likely attributable to changes in the abiotic environment following habitat conversion and fragmentation. We discuss these results and their potential drivers below.

Contrary to our predictions, we found that skink $\delta^{15}N$ values were higher in fragments and the matrix compared to continuous forest. Theory predicts that species at higher trophic levels are at greater risk of extinction (Holt 1993, 1997). Since trophic position is positively correlated with $\delta^{15}N$, loss of higher trophic level prey should result in lower $\delta^{15}N$ values in a generalist predator. This theoretical prediction emphasizes the spatial effects of fragmentation and assumes an inhospitable matrix. However, fragmentation also alters the abiotic environment (Saunders et al. 1991, Laurance et al. 2011, Tuff et al. 2016), which can affect species distribution and abundance sometimes notwithstanding of trophic level. Gut content analysis revealed that the observed shifts in skink $\delta^{15}N$ values were likely driven by higher occurrence of a primary consumer (detritivorous) prey, the terrestrial amphipod *Arcitalitrus sylvaticus*, in the continuous forest than in the fragments or matrix. This pattern is supported by studies at Wog Wog showing that amphipods during the same period as our study were, on average, over 3 and 7 times more abundant in pitfall traps from continuous forest than fragments and matrix respectively (Margules et al. 1994). These patterns show that the abiotic changes following clearing and fragmentation drastically reduced the abundance of amphipods by making them more susceptible to desiccation because they live in and feed on decaying litter on the forest floor and require a relatively moist environment (Friend and Richardson 1986, Cowling et al. 2003). Regardless of treatment, skink diets most frequently contained spiders and ants, prey items of higher trophic level than amphipods. While, in agreement with theoretical predictions, some predatory arthropods like carabid beetles are negatively affected by fragmentation at Wog Wog, other beetle groups and scorpions are unaffected or even benefit from habitat conversion and fragmentation (Margules et al. 1994, Davies et al. 2000). Our experimental findings alter our current understanding of the ecological effects of fragmentation by showing that the impacts of fragmentation on food web structure are difficult to predict under existing theoretical frameworks as they can be driven by spatial and/or abiotic effects. Moreover, changes in trophic structure induced by fragmentation can be driven by changes in the detritus based 'brown food web', which in our case affected the abundance and distribution of a key prey (detritivorous amphipod) for skinks, rather than the typically more emphasized primary production based 'green food web'.

Skinks occurring in the pine plantation matrix had lower $\delta^{13}C$ values than those in fragments or continuous forest. Furthermore, the difference in mean $\delta^{13}C$ values between skinks in the matrix versus fragments or continuous forest increased with time since fragmentation (Supplementary material Appendix 1 Fig. A1), a pattern likely driven by lower $\delta^{13}C$ values in understory plants as the plantation matured. Monterey pines are rapidly-growing trees (McDonald and Laacke 1990) that during the time since fragmentation (2–12 yr) created an increasingly shaded and humid environment in the matrix understory resulting in slower rates of transpiration in understory plants, yielding lower foliar tissue $\delta^{13}C$ values (Cernusak et al. 2013). These baseline shifts in plant isotope values would have propagated through the food web to change the $\delta^{13}C$ values of consumers like skinks. Shifts in $\delta^{13}C$ values over time also emphasize the importance of considering the dynamics of the matrix (Laurance et al. 2011, Evans et al. 2017).

We found that overall the size of the isotopic niche was larger in the fragments and matrix compared to the continuous forest. However, these changes in the size of the skink's niche are largely driven by changes in baseline (plant) $\delta^{13}C$ values of the pine plantation matrix over time that are described above and are inconsistent across time intervals. Our findings contrast with a study that found that fragmentation reduced the size of an aquatic generalist predator's (grey snapper) isotopic niche (Layman et al. 2007b). The discrepancy between our findings and those of Layman et al. (2007b) are likely because the previous study found that fragmentation converted a once diverse tidal creek ecosystem into one dominated by a microalgal mat, which severely restricted the diversity and trophic level of prey available to snappers. In contrast, the degrading impacts of habitat fragmentation on arthropod food web structure at Wog Wog are comparatively much less severe.

Given that dynamics of the matrix surrounding fragments is key in mediating fragmentation effects (Resasco et al. 2017a), it is important to consider that fragmented landscapes with different matrix types likely exhibit different responses than those observed in this study. Other fragmentation experiments could provide further insight. For example, the experimental design of the Stability of Altered Forest Ecosystems (SAFE) Project in Borneo (Ewers et al. 2011), is embedded in a gradient of land-use intensity and could this provide further insight into the role of the matrix in mediating fragmentation effects on species' niches.

What does our work teach us about how fragmentation alters trophic structure and species' niches? There are two major conclusions. First, shifts in isotopic niches captured important changes in a generalist predator's trophic position and abiotic environment following habitat fragmentation. Thus, because variation in an organism's isotopic composition is linked naturally to its niche, isotope analysis of generalist consumers like skinks can help us to better understand how key biotic and abiotic processes change when landscapes are fragmented. Second, fragmentation can affect organisms via spatial effects (e.g. isolation of small populations) or by altering environmental conditions (e.g. via edge effects). The potential importance of spatial and/or environmental effects at different trophic levels makes it difficult to predict how fragmentation will affect trophic structure in fragmented landscapes. This finding highlights the importance of rethinking models of fragmentation and their assumptions

and including abiotic effects and matrix dynamics into theory to better depict fragmentation effects on organisms and food webs.

Acknowledgements – We thank CSIRO researchers for collection of pitfall data and CSIRO's Australian National Wildlife Collection for permission to collect samples from museum specimens.
Funding – This work was funded by an NSF Postdoctoral Research Fellowship in Biology (DBI 1309192) to JR and NSF funding (DEB 0841892) to KFD and BAM and (DEB 1350872) to KFD.

References

Anderson, L. and Burgin, S. 2002. Influence of woodland remnant edges on small skinks (Richmond, New South Wales). – Austral Ecol. 27: 630–637.
Aranda, I. et al. 2007. Water-use efficiency in cork oak (*Quercus suber*) is modified by the interaction of water and light availabilities. – Tree Physiol. 27: 671–677.
Austin, M. P. and Nicholls, A. O. 1988. Species associations within herbaceous vegetation in an Australian eucalypt forest. – In: During, H. J. et al. (eds), Diversity and pattern in plant communities. SPB Academic, pp. 95–114.
Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.
Bearhop, S. et al. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. – J. Anim. Ecol. 73: 1007–1012.
Brudvig, L. A. et al. 2017. Evaluating conceptual models of landscape change. – Ecography 40: 74–84.
Bugoni, L. et al. 2008. Effects of preservation methods on stable isotope signatures in bird tissues. – Rapid Commun. Mass Spect. 22: 2457–2462.
Cernusak, L. A. et al. 2013. Environmental and physiological determinants of carbon isotope discrimination in terrestrial plants. – New Phytol. 200: 950–965.
Chapin, F. S. et al. 1997. Biotic control over the functioning of ecosystems. – Science 277: 500–504.
Chase, J. M. and Leibold, M. A. 2003. Ecological niches: linking classical and contemporary approaches. – Univ. of Chicago Press.
Collinge, S. K. 2009. Ecology of fragmented landscapes. – Johns Hopkins Univ. Press.
Cowling, J. E. et al. 2003. Environmental tolerances of an invasive terrestrial amphipod, *Arcitalitrus dorrieni* (Hunt) in Britain. – Comp. Biochem. Physiol. A 136: 735–747.
Davies, K. F. et al. 2000. Which traits of species predict population declines in experimental forest fragments? – Ecology 81: 1450–1461.
Debinski, D. M. and Holt, R. D. 2000. A survey and overview of habitat fragmentation experiments. – Conserv. Biol. 14: 342–355.
DeNiro, M. J. and Epstein, S. 1978. Influence of diet on distribution of carbon isotopes in animals. – Geochim. Cosmochim. Acta 42: 495–506.
Ehleringer, J. R. et al. 1993. Stable isotopes and plant carbon/water relations. – Academic Press.
Estes, J. A. et al. 2011. Trophic downgrading of planet Earth. – Science 333: 301–306.
Evangelista, C. et al. 2014. Ecological opportunities and intraspecific competition alter trophic niche specialization in an opportunistic stream predator. – J. Anim. Ecol. 83: 1025–1034.
Evans, M. J. et al. 2017. Short- and long-term effects of habitat fragmentation differ but are predicted by response to the matrix. – Ecology 98: 807–819.
Ewers, R. M. and Didham, R. K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. – Biol. Rev. 81: 117–142.
Ewers, R. M. et al. 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. – Phil. Trans. R. Soc. B 366: 3292–3302.
Fischer, J. and Lindenmayer, D. B. 2006. Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. – Oikos 112: 473–480.
Foley, J. A. et al. 2007. Our share of the planetary pie. – Proc. Natl Acad. Sci. USA 104: 12585–12586.
Foley, J. A. et al. 2011. Solutions for a cultivated planet. – Nature 478: 337–342.
Friend, J. A. and Richardson, A. M. M. 1986. Biology of terrestrial amphipods. – Annu. Rev. Entomol. 31: 25–48.
Gannes, L. Z. et al. 1998. Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. – Comp. Biochem. Phys. A 119: 725–737.
Gibb, H. and Cunningham, S. A. 2011. Habitat contrasts reveal a shift in the trophic position of ant assemblages. – J. Anim. Ecol. 80: 119–127.
Gravel, D. et al. 2011. Trophic theory of island biogeography. – Ecol. Lett. 14: 1010–1016.
Haddad, N. M. et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. – Sci. Adv. 1: E1500052.
Harrison, S. and Bruna, E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? – Ecography 22: 225–232.
Henle, K. et al. 2004. Predictors of species sensitivity to fragmentation. – Biodivers. Conserv. 13: 207–251.
Hobbs, R. J. 1993. Effects of landscape fragmentation on ecosystem processes in the Western-Australian wheatbelt. – Biol. Conserv. 64: 193–201.
Hobbs, R. J. 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. – Conserv. Biol. 15: 1522–1528.
Hobson, K. A. and Clark, R. G. 1992. Assessing avian diets using stable isotopes. 1. Turnover of C-13 in tissues. – Condor 94: 181–188.
Hobson, K. A. et al. 1997. Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotope analysis. – Can. J. Zool. 75: 1720–1723.
Hoekstra, J. M. et al. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. – Ecol. Lett. 8: 23–29.
Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities: historical and geographical perspectives. Univ. of Chicago Press, pp. 77–88.
Holt, R. D. 1997. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. – In: Hanski, I. P. and Gilpin, M. E. (eds), Metapopulation

dynamics: ecology, genetics, and evolution. Academic Press, pp. 149–164.
Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. – Proc. Natl Acad. Sci. USA 106: 19659–19665.
Holt, R. D. and Hoopes, M. F. 2005. Food web dynamics in a metacommunity context. – In: Holyoak, M. et al. (eds), Metacommunities: spatial dynamics and ecological communities. Univ. of Chicago Press, pp. 68–93.
Hutchinson, G. E. 1957. Population studies – animal ecology and demography – concluding remarks. – Cold Spring Harb. Symp. 22: 415–427.
Hutchinson, G. E. 1978. An Introduction to population ecology. – Yale Univ. Press.
Jackson, A. L. et al. 2011. Comparing isotopic niche widths among and within communities: SIBER – stable isotope bayesian ellipses in R. – J. Anim. Ecol. 80: 595–602.
Jones, H. I. and Resasco, J. 2016. A new species of *Hedruris* (Nematoda: Hedruridae) from the Australian skink *Lampropholis guichenoti* (Reptilia: Scincidae). – Comp. Parasitol. 83: 173–176.
Komonen, A. et al. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. – Oikos 90: 119–126.
Kosmidis, I. 2013. brglm: bias reduction in binary-response generalized linear models. – R package ver. 0.5-9.
Krab, E. J. et al. 2012. Reservations about preservations: storage methods affect delta C-13 signatures differently even in closely related soil fauna. – Methods Ecol. Evol. 3: 138–144.
Laurance, W. F. et al. 2011. The fate of Amazonian forest fragments: a 32-year investigation. – Biol. Conserv. 144: 56–67.
Layman, C. A. et al. 2007a. Can stable isotope ratios provide for community-wide measures of trophic structure? – Ecology 88: 42–48.
Layman, C. A. et al. 2007b. Niche width collapse in a resilient top predator following ecosystem fragmentation. – Ecol. Lett. 10: 937–944.
Lunney, D. et al. 1989. Diets of scincid lizards *Lampropholis guichenoti* (Dumeril and Bibron) and *Lampropholis delicata* (De Vis) in Mumbulla State Forest on the South Coast of New South Wales. – Aust. Wildl. Res. 16: 307–312.
Margules, C. R. 1992. The Wog-Wog habitat fragmentation experiment. – Environ. Conserv. 19: 316–325.
Margules, C. R. et al. 1994. Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and an amphipod. – Ecology 75: 2033–2042.
Martinson, H. M. and Fagan, W. F. 2014. Trophic disruption: a meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. – Ecol. Lett. 17: 1178–1189.
Matias, M. G. et al. 2017. Divergent trophic responses to biogeographic and environmental gradients. – Oikos 126: 101–110.
McCann, K. S. 2000. The diversity-stability debate. – Nature 405: 228–233.
McDonald, P. M. and Laacke, R. J. 1990. Monterey pine, *Pinus radiata* D. Don. – In: Burns, R. M. and Honkala, B. H. (eds), Silvics of North America: agriculture handbook 654. USDA Forest Service, pp. 433–441.
Morales-Castilla, I. et al. 2015. Inferring biotic interactions from proxies. – Trends Ecol. Evol. 30: 347–356.
National Forest Inventory 2013. Australia's State of the Forests Report. – Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES).
Newsome, S. D. et al. 2007. A niche for isotopic ecology. – Front. Ecol. Environ. 5: 429–436.
Oksanen, J. et al. 2010. Vegan: community ecology package. – R package ver. 1.17-1.
Pereira, H. M. et al. 2010. Scenarios for global biodiversity in the 21st century. – Science 330: 1496–1501.
Petchey, O. L. et al. 1999. Environmental warming alters food-web structure and ecosystem function. – Nature 402: 69–72.
Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. – Ecology 83: 703–718.
Post, D. M. et al. 2000. Ecosystem size determines food-chain length in lakes. – Nature 405: 1047–1049.
Post, D. M. et al. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. – Oecologia 152: 179–189.
Resasco, J. et al. 2012. Habitat corridors alter relative trophic position of fire ants. – Ecosphere 3: art100.
Resasco, J. et al. 2017a. The contribution of theory and experiments to conservation in fragmented landscapes. – Ecography 40: 109–118.
Resasco, J. et al. 2017b. Data from: Generalist predator's niche shifts reveal ecosystem changes in an experimentally fragmented landscape. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.56b81>.
Ryall, K. L. and Fahrig, L. 2006. Response of predators to loss and fragmentation of prey habitat: a review of theory. – Ecology 87: 1086–1093.
Sala, O. E. et al. 2000. Global biodiversity scenarios for the year 2100. – Science 287: 1770–1774.
Sarakinos, H. C. et al. 2002. A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. – Can. J. Zool. 80: 381–387.
Saunders, D. A. et al. 1991. Biological consequences of ecosystem fragmentation: a review. – Conserv. Biol. 5: 18–32.
Schmidt, S. N. et al. 2007. Quantitative approaches to the analysis of stable isotope food web data. – Ecology 88: 2793–2802.
Schoener, T. W. 1989. Food webs from the small to the large. – Ecology 70: 1559–1589.
Takimoto, G. et al. 2008. Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. – Ecology 89: 3001–3007.
Taylor, R. 2015. Chapter 5: saving forests at risk. – In: Taylor, R. (ed.), WWF Living Forests Report, <www.worldwildlife.org/publications/living-forests-report-chapter-5-saving-forests-at-risk>.
Terborgh, J. and Estes, J. A. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. – Island Press.
Terborgh, J. et al. 2001. Ecological meltdown in predator-free forest fragments. – Science 294: 1923–1926.
Tuff, K. T. 2016. On taking a thermal approach to fragmentation research. – Univ. Colorado at Boulder.
Tuff, K. T. et al. 2016. A framework for integrating thermal biology into fragmentation research. – Ecol. Lett. 19: 361–374.
Vander Zanden, M. J. et al. 1999. Patterns of food chain length in lakes: a stable isotope study. – Am. Nat. 154: 406–416.

Vander Zanden, M. J. et al. 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. – PLoS One 10: e0116182.
Vanderklift, M. A. and Ponsard, S. 2003. Sources of variation in consumer-diet delta(15)N enrichment: a meta-analysis. – Oecologia 136: 169–182.
Vitousek, P. M. et al. 1997. Human domination of Earth's ecosystems. – Science 277: 494–499.

Supplementary material (Appendix ECOG-03476 at < www.ecography.org/appendix/ecog-03476 >). Appendix 1.

Warne, R. W. et al. 2010. Tissue-carbon incorporation rates in lizards: implications for ecological studies using stable isotopes in terrestrial ectotherms. – Physiol. Biochem. Zool. 83: 608–617.
Wilcove, D. S. et al. 1998. Quantifying threats to imperiled species in the United States. – Bioscience 48: 607–615.
Wilson, S. K. 2012. Australian lizards: a natural history. – CSIRO Publishing.