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Experimental habitat fragmentation disrupts nematode infections in Australian skinks

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Abstract. Habitat conversion and fragmentation threaten biodiversity and disrupt species interactions. While parasites are recognized as ecologically important, the impacts of fragmentation on parasitism are poorly understood relative to other species interactions. This lack of understanding is in part due to confounding landscape factors that accompany fragmentation. Fragmentation experiments provide the opportunity to fill this knowledge gap by mechanistically testing how fragmentation affects parasitism while controlling landscape factors. In a large-scale, long-term experiment, we asked how fragmentation affects a host–parasite interaction between a skink and a parasitic nematode, which is trophically transmitted via a terrestrial amphipod intermediate host. We expected that previously observed amphipod declines resulting from fragmentation would result in decreased transmission of nematodes to skinks. In agreement, we found that nematodes were absent among skinks in the cleared matrix and that infections in fragments were about one quarter of those in continuous forest. Amphipods found in gut contents of skinks and collected from pitfall traps mirrored this pattern. A structural equation model supported the expectation that fragmentation disrupted this interaction by altering the abundance of amphipods and suggested that other variables are likely also important in mediating this effect. These findings advance understanding of how landscape change affects parasitism.

Key words: *Australia; biodiversity; fragmentation experiment; habitat fragmentation; habitat loss; Hedreris; Lampropholis guichenoti; lizard; nematode; parasite; skink; Wog Wog.*

INTRODUCTION

Habitat conversion and fragmentation are widespread impacts of humans on landscapes that drive biodiversity loss and disrupt species interactions (Wilcove et al. 1998, Tylianakis et al. 2008, Butchart et al. 2010). Parasites have been suggested to be particularly at risk due to cascading effects of species loss (i.e., coextinction; Dunn et al. 2009, Lafferty 2012). While there is a growing realization that parasites play important roles in food webs and ecosystem processes (Hudson et al. 2006, Dobson

et al. 2008, Kuris et al. 2008, Lafferty et al. 2008), the effects of fragmentation on parasitism vary among studies (Taylor and Merriam 1996, Allan et al. 2003, Mborá and McPeck 2009, Sullivan et al. 2011, Gottdenker et al. 2014, Bordes et al. 2015) and the underlying mechanisms are poorly understood compared to other species interactions (Hagen et al. 2012, Martinson and Fagan 2014).

Limited understanding of fragmentation effects on parasitism could be attributed to a scarcity of experimental studies (Gottdenker et al. 2014) as well as the complexity of parasite life cycles, variation in species responses to fragmentation, and confounded landscape variables. For example, trophically transmitted helminths may require multiple different obligate hosts over the course of their life cycle (Olsen 1974) and thus fragmentation could affect transmission of parasites via responses of

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intermediate host populations (Bordes et al. 2015). These responses of populations to fragmentation can conceivably be positive, negative, or neutral (Fahrig 2003). Fragmentation can affect species by various mechanisms, including altering dispersal of individuals between fragments, environmental conditions, and populations of other interacting species (Saunders et al. 1991). Disentangling the effects of fragmentation on parasitism is further complicated by landscape factors, such as disturbance type, area of impact, and non-random conversion of habitat; these factors are difficult to tease apart in most fragmented landscapes (Didham et al. 2012). Long-term fragmentation experiments that manipulate landscape

configuration and monitor populations and communities can provide solutions to some of these issues (Debinski and Holt 2000, Collinge 2009, Haddad et al. 2015) and allow for a more mechanistic understanding of the effects of fragmentation on parasitism.

We used the large-scale Wog Wog Habitat Fragmentation Experiment (Fig. 1A) to determine the effects of fragmentation on a host–parasite interaction. The pale-flecked garden sunskink (*Lampropholis guichenoti*, referred to as “skink”) hosts a nematode parasite (*Hedruris wogwogensis*, referred to as “nematode”) that is trophically transmitted via a crustacean intermediate host (the terrestrial amphipod *Arcitalitrus sylvaticus*,

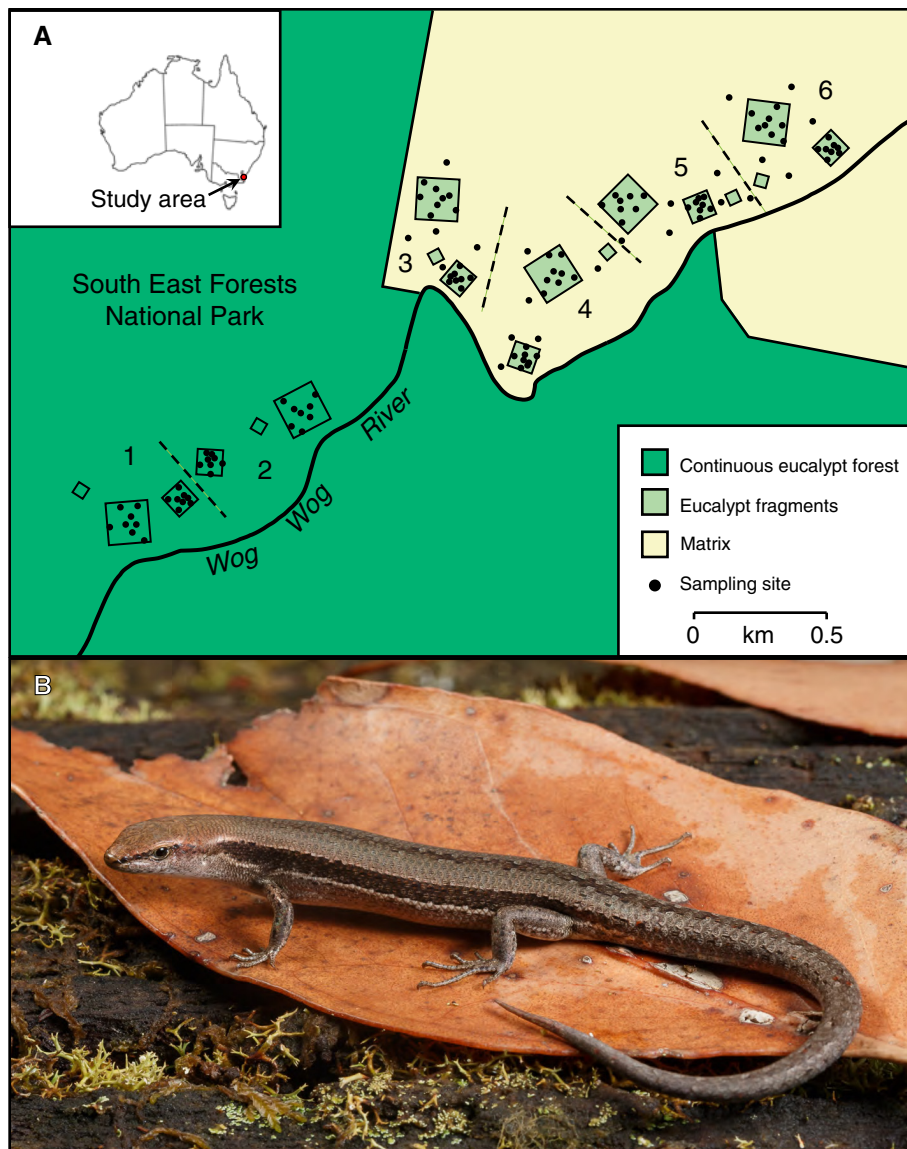


FIG. 1. (A) Wog Wog Habitat Fragmentation Experiment (modified from Resasco et al. 2018). Dark green areas represent continuous eucalypt forest, light green areas represent eucalypt forest fragments, and yellow areas represent the matrix (cleared eucalypt forest converted into a pine plantation). Dots represent pitfall sampling sites. Sampling sites on small fragments are not shown because of space constraints. (B) Pale-flecked garden sunskink (*Lampropholis guichenoti*; photo credit: Jules Farquhar).

referred to as “amphipod”; Jones and Resasco 2016). We necropsied skinks to determine how fragmentation affected infection by nematodes and prevalence of amphipods in their diet. We then examined pitfall trap counts of amphipods and skinks during the same study period and related these counts to nematode infection in skinks. Further, we necropsied amphipods to confirm their role as intermediate hosts for these nematodes.

How might a trophically transmitted parasite be affected by fragmentation? By placing our existing knowledge of the Wog Wog system in the framework of existing ecological theory, we can generate predictions (Ryall and Fahrig 2006). Bascompte and Solé’s (1998) model for predator–prey dynamics in a donor-controlled scenario shows that predators decline sharply as their prey decline with habitat loss and fragmentation. These predictions could apply to our study, with amphipods being analogous to prey and the parasitic nematodes being analogous to specialist predators in a donor-controlled scenario since they are specialist parasites on the focal amphipods and skinks but may not exert strong top-down control on their hosts’ populations. From previous studies at Wog Wog, we know that fragmentation led to declines in pitfall trap captures of amphipods (Margules et al. 1994) and a decline in their incidence in the diet of skinks (Resasco et al. 2018). Declines in the intermediate host caused by fragmentation could disrupt the parasite’s life cycle (Lafferty 2012) and thus its transmission to the final host. Given this theory and previous findings from our system, we hypothesized that the transmission of nematodes to skinks should be disrupted by fragmentation via declines in the amphipod intermediate hosts. Because final host density could also affect the parasite’s life cycle, we also examined whether fragmentation affected nematode transmission via effects on skink densities.

METHODS

The Wog Wog Habitat Fragmentation Experiment is located in New South Wales, Australia (37°04′30″ S, 149°28′00″ E; Fig. 1A) and was designed to test the ecological effects of forest fragmentation (Margules 1992). The experimental fragmenting of the forest took place in 1987 by clearing eucalypt forest, leaving behind fragments, and planting the cleared matrix into a pine plantation. The experiment consists of eucalypt forest fragments of three sizes, 0.25 ha (small), 0.875 ha (medium), and 3.062 ha (large), in four blocks (12 fragments total). Two blocks of the same layout are delineated as plots within an adjacent continuous eucalypt forest that serve as a control reference stand (Fig. 1A). At Wog Wog, invertebrates were monitored using pitfall traps at permanent sampling sites between 1985 (2 yr prior to fragmentation) and 1999 and from 2010 to 2018, referred to hereafter as first and second sampling periods, respectively. Pitfall traps were opened for seven days during each season in 1985–1999, in each season except

winter from 2010 to 2013, summer and autumn 2015, summer 2016, and summer 2018. Each pitfall trap sampling site consisted of paired 90-mm diameter pitfall traps (5–10 m apart). Skinks were collected as accidental bycatch in pitfall traps and all individuals ($n = 186$) were stored in a 3:1 ethanol:water solution at the CSIRO Australian National Wildlife Collection. Within each patch (fragment or plot within the continuous eucalypt forest), there were eight sampling sites that were stratified by topography and proximity to the fragment edge. There were an additional 44 sampling sites in matrix between fragments (Fig. 1A). A full description of the experimental design and sampling methods can be found in Margules (1992).

The skink, *Lampropholis guichenoti* (Fig. 1B), is common and widespread in eastern Australia. It is a generalist consumer and a habitat generalist (Lunney et al. 1989, Wilson 2012, Resasco et al. 2018). At Wog Wog, these skinks were common across sampled habitats (continuous eucalypt forest, eucalypt fragments, and matrix) during the first sampling period (Tuff 2016). They maintain relatively small home ranges of approximately 20 m² (Anderson and Burgin 2002), which are well matched to the spatial scale of the experiment.

As part of another study (Resasco et al. 2018), we collected guts (foregut, hindgut, and stomach) from adult museum specimens of these skinks from the experiment to examine prey items. These selected specimens represented nearly all of the 188 sampling sites from 1988–1997, approximately 2–12 yr post fragmentation (mean \pm SD = 7 \pm 2.4 yr). We stored skink guts in 75% ethanol and subsequently removed gut contents and identified parasites and prey to the finest taxonomic resolution feasible. The nematode *Hedruris wogwogensis* was common in the guts of the sampled skinks (Jones and Resasco 2016).

Nematodes in the genus *Hedruris* (family Hedruridae) infect fishes, amphibians, and reptiles (Anderson 2000, Jones and Resasco 2016). These nematodes are known to have trophic transmission and use single species of crustaceans (amphipods and isopods) as intermediate hosts (Anderson 2000, Luque et al. 2010, Casalins et al. 2015). They are known to develop into immature adults within crustaceans’ body cavities, seemingly to accelerate gamete production in the definitive host (Petter 1971). Because the terrestrial amphipod *Arcitalitrus sylvaticus* is abundant in pitfall traps (Margules et al. 1994) and are common skink prey (Resasco et al. 2018), we believed that it was likely the intermediate host for these nematodes. To determine whether amphipods serve as intermediate hosts for these nematodes, we necropsied amphipods collected in pitfall traps from the second sampling period, over nine sampling seasons from November 2009 to February 2018 and from sifted leaf litter collected in the field in January 2018. Isopods were much less abundant in pitfall traps and rarely found within skink gut contents (Resasco et al. 2018). We examined amphipods and skink guts using a Nikon SMZ1500

stereomicroscope (7.5×–112.5× magnification; Tokyo, Japan) and used morphological characteristics from Jones and Resasco (2016) for identification. Amphipod specimens from the first sampling period were not available for this assessment.

We used generalized linear models to test for a fragmentation treatment effect (levels: continuous eucalypt forest, eucalypt fragments, and matrix) on nematode and amphipod prevalence in skinks guts, specifying a binomial distribution and logit link function. For the amphipod prevalence model, we only included data from individuals in which any prey items were identifiable from gut contents (124 individuals). We fit these models using *brglm2* (bias-reduced GLMs) version 0.1.4 (Kosmidis 2017). This method was used because of complete separation of the response variable among treatments; nematodes and amphipods were absent in the guts of skinks collected in the matrix. We did not include fragment size, edge, topography, block, or time since fragmentation as variables in models due to scarcity of presence data among fragments. We used models with and without a given variable to assess the change in deviance and significance (from a likelihood ratio test) for that variable (Bolker 2008). We estimated effect sizes (log odds ratio) between both fragments and matrix compared to continuous eucalypt forest. We calculated 95% confidence intervals based on likelihood profiles. We tested for differences in intensity of parasite infection (number of nematodes among infected individuals, *sensu* Bush et al. 1997) between skinks from fragments and continuous eucalypt forest using a negative binomial linear model (no skink individuals were infected in the matrix).

To further investigate the effects of fragmentation on amphipod abundance, we used pitfall data from the first sampling period during the years for which skink gut samples were collected, 1988–1997 (Margules et al. 1994). We used generalized linear mixed models to test for fragmentation treatment effects on amphipod count data from pitfall traps, including block as a random effect. We specified a Poisson distribution with a log link function. We fit generalized linear mixed models using the R package *lme4*, version 1.1-7 (Bates et al. 2015). We used logistic regression to relate the abundance of amphipods from pitfall traps counts to the prevalence of nematode in skinks from the same traps both across and within treatments. Because nematode parasites potentially persist for years within hosts, we fit models using

amphipod abundance from the same year the skink was collected as well as with amphipod counts pooled with the previous one, two, and three years' data. We used small sample size bias corrected Akaike Information Criterion, AIC_c , to select among these models to determine the most appropriate timescale.

Finally, we used a structural equation model (SEM) to determine which causal pathways were responsible for the relationship between habitat fragmentation and nematode infection in skinks. We used piecewise SEM using the *piecewiseSEM* R package (Lefcheck 2016). We logged skink, amphipod, and nematode abundance and fitted linear mixed effects models to each response using the function *lmer* from the *lme4* package (Bates et al. 2015). Skink abundance was quantified as the number of adult individuals captured in a given pitfall trap during the same year as each examined skink. Amphipod abundance was quantified as the pooled number of individuals captured in a given pitfall trap in the same and previous three years as that of each examined skink's capture (determined by AIC_c analysis above). We included random effects of block, patch, and pitfall trap site in each model. We analyzed our data in R (R Core Team 2017).

RESULTS

We found that 18% of the skinks examined (34/186) hosted one or more nematode (Table 1). Prevalence of nematodes in skinks differed among habitat treatments ($\chi^2 = 49.0$, $df = 2$, $P < 0.001$; Fig. 2A). Among skinks in continuous eucalypt forest, 55% (23/42) contained nematodes. Among skinks in the fragments, 11% (11/99) contained nematodes. Nematode was absent among skinks in the matrix, (0/45; Table 1). Intensity of nematodes did not differ significantly between skinks in the continuous eucalypt forest (intensity = 4.4 ± 3.6 [mean \pm SD]) and fragments (intensity = 5.3 ± 5.5 ; $\chi^2 = 0.35$, $P = 0.55$; Table 1).

Counts of amphipods in pitfall traps differed among treatment ($\chi^2 = 16.6$, $df = 2$, $P < 0.001$; Fig. 2B). There were 33,876 amphipods collected in pitfall traps during the period corresponding to the skink samples examined (1988–1997). During this period, amphipods in pitfall traps from continuous eucalypt forest were on average three and seven times more abundant than those from fragments and the matrix, respectively (Table 1; Fig. 2B).

TABLE 1. Summary across fragmentation treatment levels of prevalence, intensity, and abundance of the nematode *Hedrwis wogwogensis* in the guts of the skink *Lampropholis guichenoti*, prevalence of the amphipod *Arcitalitrus sylvaticus* among individuals of skinks with identifiable prey items in their gut, and amphipod counts from pitfall traps.

Location	Nematode prevalence in skinks (%)	Nematode intensity†	Nematode abundance‡	Amphipod prevalence in skinks (%)	Amphipod counts in pitfall traps‡
Continuous eucalypt forest	55% (23/42)	4.4 ± 3.6	2.4 ± 3.4	31% (10/32)	396 ± 184
Eucalypt fragments	11% (11/99)	5.3 ± 5.5	0.6 ± 2.4	9% (6/65)	129 ± 163
Matrix	0% (0/45)		0	0% (0/27)	56 ± 58

†Mean \pm SD.

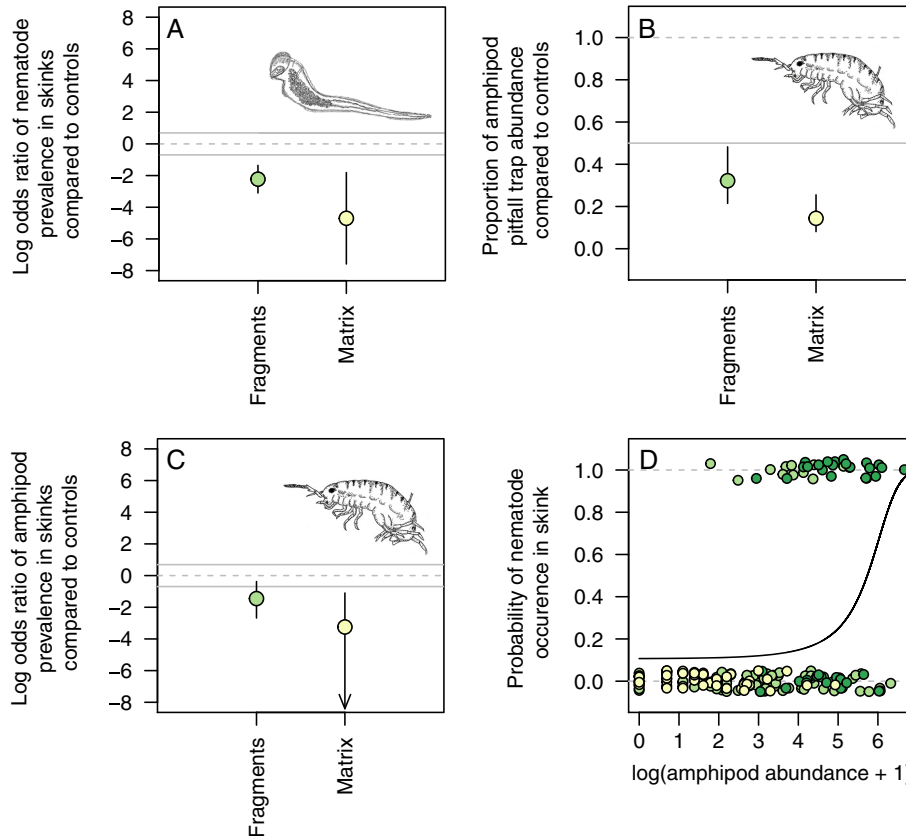


FIG. 2. (A) Effect sizes (log odds ratio \pm 95% CIs) for responses to habitat conversion and fragmentation for prevalence of the nematode *Hedruris wogwogensis* in the skink *Lampropholis guichenoti*. Light green circles indicate effect sizes for fragments while yellow circles indicate effect sizes for the matrix, both relative to continuous eucalypt forests controls. Solid gray horizontal lines represent either a doubling or halving in the odds of occurrence. (B) Effect sizes (\pm 95% CIs) for abundance of the amphipod *Arcitalitrus sylvaticus* in pitfall traps during the study period. Effects correspond to amphipod abundance in pitfall traps from fragments and the matrix being 32% and 14% as high as those in the continuous eucalypt forest, respectively. The solid gray horizontal line represents a halving in abundance. (C) Effect sizes (log odds ratio \pm 95% CIs) for the prevalence of amphipods in skinks. The downward pointing arrow indicates a confidence limit that extends to infinity (due to the total absence of the amphipod in skinks sampled from the matrix). (D) Probability of occurrence of nematodes in skinks as a function of amphipod pitfall trap counts. Points represent pitfall trap sites with their color representing treatments. Dark green dots represent continuous eucalypt forest, light green represent fragments, and yellow represent the matrix. Points are jittered to reduce overlap. The x-axis is log-transformed for visualization purposes. Drawing in A is by Hugh I. Jones. Drawing in B and C is by Marilina Pratt from a photo by Ken Walker.

Prevalence of amphipods in skinks differed among treatment ($\chi^2 = 14.6$, $df = 2$, $P < 0.001$; Fig. 2C). Among skinks in continuous eucalypt forest with identifiable prey items in their gut, 31% (10/32) contained amphipods. Amphipods were much less common as prey items in fragments. Among skinks in fragments with identifiable prey items in their gut, 9% (6/65) contained amphipods. Amphipods were absent as prey items for skinks in the matrix (Table 1; Fig. 2C).

Necropsies of 4,902 amphipods collected from pitfall traps from the second sampling period and from litter sifting yielded 31 immature individuals of nematodes. Amphipod individuals collected by litter sifting had a higher prevalence of nematode infection (4.5%, 3/67) than individuals collected by pitfall traps (0.2%, 11/4835). Most infected amphipods contained a single

nematode (71%, 10/14), but a few contained multiple nematodes (maximum intensity = 14).

The best model relating pitfall trap amphipod counts to nematodes in skinks (i.e., the logistic regression with the lowest AIC_c value) included the last four years of amphipod counts. This model was 7.2 AIC_c values lower than the next best model, which included the last three years of amphipod counts. Amphipod counts were positively associated with nematode prevalence in skinks (Fig. 2D; coefficient = 0.007, log odds ratio = 1.007, $z = 4.2$, $P < 0.001$). However, within treatments, there was no significant association (fragments: coefficient < 0.001 , log odds ratio = 1.000, $z = 0.01$, $P = 1.00$; continuous eucalypt forest: coefficient = 0.006, log odds ratio = 1.006, $z = 1.9$, $P = 0.06$; nematodes were absent from skinks collected in the matrix).

The causal pathway and results for the piecewise SEM analysis are presented in Fig. 3. There are three key findings: (1) habitat fragmentation had a large effect on amphipod abundance, which, in turn, determined nematode abundance in skinks. Because the effect of fragmentation on amphipod abundance was large, the overall impact on nematode abundance was large, even though the direct effect of amphipod abundance on nematode abundance was comparatively small. (2) Habitat fragmentation positively affected skink abundance but skink abundance did not impact nematode abundance in skinks. (3) Fragmentation had a large effect on nematode abundance in skinks, aside from the effect of amphipod abundance on nematode abundance. This suggests that additional unmeasured variables could be important in contributing to fragmentation impacts on nematode abundance.

DISCUSSION

Our study reveals a mechanism for how fragmentation can disrupt parasitism: by altering the abundance and distribution of an intermediate host and thus trophic transmission to the definitive host. Amphipod abundances and prevalence in skink diets were reduced by forest fragmentation. In particular, disturbances from clearing, bulldozing, and burning in the matrix negatively impacted the abundance of amphipods in the matrix and fragments. These amphipods live in leaf litter and require a relatively moist and shaded environment because they are susceptible to desiccation (Margules et al. 1994). These changes in amphipod abundance result in diet shifts by skinks (Resasco et al. 2018) and thus disrupted transmission of this nematode. These findings align with theory based on donor-controlled predator–prey scenarios under habitat loss and fragmentation (Bascompte

and Solé 1998). Our SEM analysis supported the expectation that fragmentation disrupted this host–parasite interaction by altering the abundance of amphipods but also suggested that other variables are likely also important in mediating this effect, for example, environmental variables that could affect nematode survival during its life stage in soil.

Recent findings from Wog Wog show that the responses of amphipods to habitat fragmentation treatments have changed over the long-term with maturation of the pine plantation in the matrix (Bitters et al., *unpublished data*). As the pine matrix has matured, amphipod abundances in the matrix and fragments have returned, and now they are approximately equal to the continuous eucalypt forest. With increased abundance of amphipods in the matrix, we predict that infections of skinks in the matrix will eventually approximate that of skinks in fragments and continuous eucalypt forest. We plan to test this in future work.

Fragmentation effects on intermediate hosts may be a common mechanism of disruption of host–parasite interactions. A study by Bordes et al. (2015) examined the effects of fragmentation on rodent–helminth parasite networks and found that although rodents and parasite species richness are often robust to fragmentation, connectance of the host–parasite network is reduced with fragmentation. The authors attribute the reduction of these links to fragmentation effects on populations of arthropod intermediate hosts. Our findings are consistent with this idea.

Other studies have found that fragmentation increases the prevalence of parasites and pathogens by increasing densities of hosts. Mbora and McPeck (2009) found that forest fragmentation and degradation increased densities of primate hosts and exposure to human pathogens, which increased parasite richness and prevalence. Allan et al.

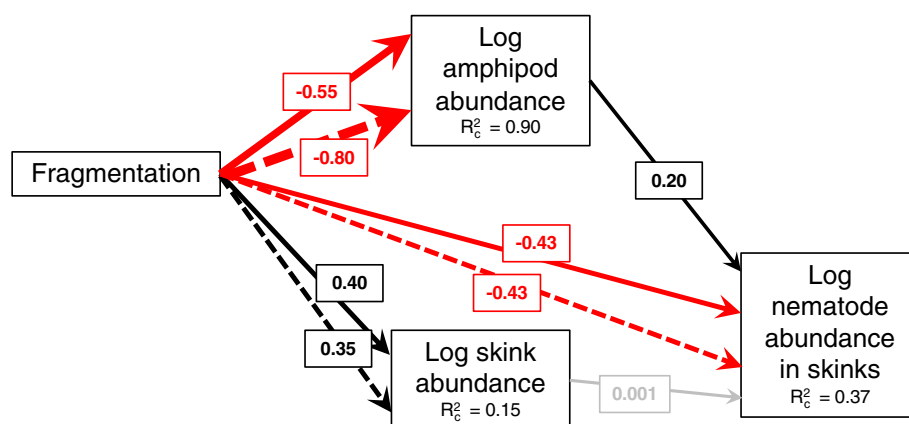


FIG. 3. Results from the piecewise structural equation model (SEM) exploring the effects of habitat fragmentation on nematode (*Hedruris wogwogensis*) infection in the final skink host (*Lampropholis guichenoti*). The amphipod *Arcitalitrus sylvaticus* is the intermediate host. Large boxes represent observed variables. R^2 values for component models are shown (R^2_c , based on both fixed and random effects). Arrows represent relationships among variables. Black arrows represent positive relationships, and red arrows negative relationships. Solid lines represent fragments compared to controls and dashed lines represent the matrix compared to controls. Arrows for nonsignificant paths ($P \geq 0.05$) are semi-transparent. Line thickness of significant paths has been scaled based on the magnitude of the standardized regression coefficients, which are presented in small boxes over the arrows.

(2003) found that fragmentation increased incidence of black-legged tick nymphs (*Ixodes scapularis*) infected by Lyme bacteria (*Borrelia burgdorferi*) by increasing densities of the principal natural reservoir for the disease, white-footed mice (*Peromyscus leucopus*). Although we found, conversely, that fragmentation reduced the prevalence of parasites, like these studies, our finding was the result of population changes of hosts within parasite life cycles.

Our findings advance understanding of how landscape change affects parasitism, showing that fragmentation can disrupt host–parasite dynamics by altering the distribution and abundance of intermediate hosts. In the context of previous work, we see that fragmentation can result in shifts in abundance and distribution of key players in host–parasite life cycles. These shifts can result in greater infection or conversely disruption of host–parasite interactions. Further understanding of how changes in landscapes cascade to affect host–parasite interactions could have important implications for disease transmission and conservation of imperiled species, both parasites and hosts.

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DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.js46h10>