RESEARCH ARTICLE



The dynamic matrix predicts population response to long-term experimental forest fragmentation

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Abstract

Context Earth's forests are fragmented. Species' long-term persistence depends on their conservation in fragmented landscapes with remnants embedded in a matrix of human land use. This matrix influences species' persistence in fragments by determining their degree of isolation and the extent to which edge effects alter habitat. Matrix habitat is often dynamic, so its impact on persistence of remnant species changes over time.

Objectives Previous research showed that the abundance response of predatory beetle species to matrix habitat predicted their response in fragments with a log-response ratio of about 0.5. When abundance declined in the matrix, there was a smaller but

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M. E. Bitters e-mail: matthew.bitters@colorado.edu

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S. Holtz e-mail: sholtz1@uwyo.edu predictable decline in fragments. However, the predictive utility of a fragment:matrix log-response ratio needs testing with functionally different species, more detailed data, and a focus on mechanism.

Methods In the Wog Wog habitat fragmentation experiment, we follow a detritivorous amphipod 27 years after forest fragmentation.

Results The amphipod's response in habitat fragments was predicted by its response in the matrix with a log-response ratio of about 0.5, similar to predatory beetles. The amphipod's response was explained by its abiotic niche. The amphipod's short-term response did not predict its long-term response.

Conclusions The log-response ratio might generalize across the invertebrate food web. For two groups within the Wog Wog experiment, a species' dynamic response in matrix habitat predicted its persistence in fragments. Future work should explore the generality of this finding. With knowledge of projected land use

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S. Holtz Department of Botany, University of Wyoming, Laramie, WY 82071, USA of matrix habitat, a species' matrix response could be used for management planning.

Keywords Habitat fragmentation · Forest · Matrix · Experiment · Long-term data · Plantation · *Arcitalitrus sylvaticus* · Amphipod · Wog Wog · Australia

Introduction

Globally, forest loss and fragmentation threaten biodiversity and the ecosystem processes that sustain life (Pereira et al. 2010; Ceballos et al. 2015; Newbold et al. 2016; Betts et al. 2017; Arroyo-Rodríguez et al. 2020). One-third of forests have been cleared, and what remains is fragmented (Hansen et al. 2013; Jacobson et al. 2019). For example, 70% of forest globally is within 1 km of an edge (Haddad et al. 2015). The long-term persistence of forest species depends on their conservation in fragmented landscapes, where forest remnants are embedded in a matrix of human land use, which may not support forest species (Watling et al. 2011; Driscoll et al. 2013; Arroyo-Rodríguez et al. 2020).

In fragmented landscapes, the matrix surrounding fragments (e.g., agriculture, plantation forestry, urban development) determines species' persistence in fragments (Watling et al. 2011; Driscoll et al. 2013; Galán-Acedo et al. 2019). For example, the matrix may completely isolate populations of a given species on fragments or, at the other end of the spectrum, provide high-quality habitat (Ricketts 2001; Davies et al. 2004; Watling et al. 2011; Driscoll et al. 2013; Brudvig et al. 2017; Evans et al. 2017). That is, the same fragmented landscape may be binary (habitat/not habitat) for some species and a continuum of habitat quality for other species. For binary species, landscape fragmentation reduces large continuous populations to small populations isolated on fragments, placing these species at greater risk of stochastic extinction and making them reliant on dispersal between fragments for persistence (Caughley 1994; Hanski 1994; Bruna 1999; Hanski and Ovaskainen 2000; Brudvig et al. 2017). In contrast, species that colonize matrix habitat may thrive in fragmented landscapes (Davies et al. 2004; Watling et al. 2011; Driscoll et al. 2013; Reider et al. 2018; Galán-Acedo et al. 2019). Finally, matrix habitat can impact populations of species on fragments by changing the abiotic environment and habitat structure; for example, by altering temperature, solar radiation, and water regimes, often via edge effects (Saunders et al. 1991; Harper et al. 2005; Haddad et al. 2015; Arroyo-Rodríguez et al. 2017).

In a recent study within the Wog Wog habitat fragmentation experiment in southeastern Australia, species' responses in matrix habitat predicted their responses in forest fragments such that responses in fragments were about one half that in the matrix (Evans et al. 2017). For 11 carabid species, their responses within matrix habitat-declines or increases compared to the continuous foreststrongly predicted their responses in fragments. Across species the fragment:matrix log-response ratio (slope of the linear relationship) was 0.44 (95%) CI 0.31, 0.57). Further, species' responses changed through time so that short-term (1-5 years/generations) responses generally did not predict long-term responses (23-25 years/generations); for example, some species declined in abundance in fragments in the short-term, but then increased in abundance longterm, or vice versa. Despite these temporal changes in species' responses, the fragment:matrix log-response ratio of about one half held over time. These findings for predatory carabid beetles were attributed to the dynamic matrix, a commercial pine plantation, which grew from pine seedlings to mature trees over the course of the experiment. This result from Evans et al. (2017) suggests that species' responses to the matrix could be the key to predicting a species' longterm response to fragmentation. The predictive utility of a fragment:matrix log-response ratio needs testing with new and functionally different species and more detailed data. Exploration of the underlying mechanisms is also needed. We note that we can talk about predictions in both space and time. Here we suggest that a species' response in abundance to matrix habitat might predict its abundance in fragments within the same time period (space). Further, if we know a species' response to matrix habitat and we know how matrix habitat will be managed, we could predict its response in abundance in both the matrix and fragments in the future (time).

Here, we quantify the fragment:matrix logresponse ratio in the same fragmentation experiment, for a longer time series, in an abundant, terrestrial amphipod, *Arcitalitrus sylvaticus*. In contrast to the predatory carabids, this amphipod is a detritivore, and a similar fragment:matrix log-response ratio would provide evidence that the ratio generalizes across the invertebrate food web regardless of trophic position. The amphipod is a key detritivore due to its large biomass in this forest system (Margules et al. 1994; Resasco et al. 2018, 2019) and is the species with the longest time series available within the Wog Wog experiment (17 time points over 27 years, at least 27 generations, after fragmentation). Further, using field data, we explore how dynamically-changing matrix habitat could underlie the existence of the log-response ratio through the abiotic niche of the amphipod. We conjecture a priori that the amphipod's abiotic niche determines its response in fragments as the matrix habitat transforms from pine seedlings to mature trees over 27 years. We expect abiotic conditions in the matrix to determine both (1) the degree of isolation of amphipod populations on fragments and/ or the size of amphipod populations in the matrix, and (2) the suitability of fragment habitat for amphipods since abiotic conditions in the matrix affect abiotic conditions and habitat structure on fragments (e.g., solar radiation and moisture content) especially at edges. We thus expect fragmentation to affect amphipod abundance in fragments both via isolation and reduced population size, and via changes to fragment habitat according to the match of the amphipod's abiotic niche with abiotic conditions in the matrix over time. While the data here are from a controlled experiment, most naturally-fragmented landscapes also contain matrix habitat that is dynamic; for example, crops or plantation timber that change in time. Thus, understanding the potential predictive role of this dynamic matrix may be critical for forecasting the persistence of species under projected dynamic land use, which could lead to targeted management strategies (Arroyo-Rodríguez et al. 2020).

Methods

The Wog Wog experiment is located in southeastern New South Wales, Australia, 17 km southeast of Bombala (37° 04′ 30″ S, 149°28′ 00″ E; Fig. 1 and Fig. S1). Wog Wog was established in 1984 and was conceived as an experiment that would run over many decades. The experimental design is described fully here (Margules 1993) and reiterated below.

The experiment consists of six replicates, each composed of three patch sizes (18 patches): 0.25 ha (small), 0.875 ha (medium), and 3.062 ha (large), with each subsequently larger patch 3.5 times the size of the next smallest patch. The 18 patches were marked out during the southern hemisphere summer of 1984–1985 in what was then continuous Eucalyptus forest. Sampling began in 1985, and two years of data were collected before clear-cutting. In 1987, the forest surrounding replicates 1-4 (Fig. 1) was clearcut and planted with Pinus radiata, a non-native species, as part of a commercial pine plantation, now run by Forestry Corporation NSW. Clear cutting created 12 remnant patches of Eucalyptus forest surrounded by pine plantation. Replicates 5 and 6 (Fig. 1) are maintained in adjacent continuous Eucalyptus forest as controls. The two control replicates serve as a comparison against the fragmented forest.

Within each fragment or control patch there are eight monitoring sites, which are stratified in two ways in a factorial design. First, sites are stratified by habitat type (topography) into slopes and drainage lines because the vegetation communities associated with these topographic features are different (Austin and Nicholls 1988). Slopes are characterized by a grassy understory and scattered shrubs below open eucalypt forest. Drainage lines are dominated by Kunzea, which is a small shrubby tree that forms dense stands, and Lomandra longifolia, which is a tussock-forming plant in the family Asparagaceae growing to about 50 cm in height and diameter. Second, sites were stratified by proximity to the fragment edge into edge and interior sites. There are two monitoring sites in each of the four strata (slope edge, slope interior, drainage-line edge, drainage-line interior), totaling eight sites within each patch/fragment. There are a total of 144 sites over the 18 patches/fragments. Forty-four additional sites were established in the pine plantation matrix in 1987 and are also stratified into slopes and drainage lines. At each site, two pitfall traps were installed at random locations within a 5 m radius of a central site marker.

Study species

Arcitalitrus sylvaticus, "lawn shrimp," are a species of amphipod in the family Talitridae and are found throughout southeastern Australia. These terrestrial crustaceans live in, and feed on, the top layer of leaf Fig. 1 Map of the experimental site. There are eight sampling sites within each patch, each with two pitfall traps. Each dot in the pine matrix represents a pair (slope plus drainage line) of sampling sites. Patch sizes are 0.25 ha, 0.875 ha and 3.062 ha. Patches are separated by at least 50 m. The eight sampling sites within each small patch are not represented because of space constraints. See Fig. S1 for a detailed spatiallyaccurate map. Right panel, I inner fragment, e fragment edge, s slope, d drainage line. Dashed lines delineate drainage lines



litter and must remain moist to avoid desiccation (Margules et al. 1994). At Wog Wog, they are most abundant in forested habitat with an understory dominated by *Lomandra longifolia*, an evergreen perennial herb that occupies drainage lines (Margules et al. 1994). Adult *A. sylvaticus* range in size from 5 to 20 mm.

Data collection

Invertebrates were sampled four times per year from 1985 to 1998, once during each season, November (spring), February (summer), May (autumn), and June (winter), and three times per year from 2009 to 2014 (each season excluding winter). Pitfall traps were opened for seven days during each sampling period. Traps were 8.5 cm diameter, 475 ml plastic cups filled with a 150 ml solution of 75% ethanol (95%), and 25% glycol. Samples for the two traps at

each monitoring site were pooled. Amphipods were identified and counted in the laboratory.

Temperature data were collected using data loggers with an integrated sensor (Onset Corporation, model UA-002-64) from November 2011 to May 2012 and from November 2012 to May 2013 at 20-min intervals. Data loggers were placed one meter north of the center of each site marker and attached to a plastic stake at 5 cm off the ground. Temperature sampling spanned spring, summer, and fall to account for seasonal differences in thermal conditions and 2 years to account for annual variation.

To quantify canopy cover, upward-facing photographs were taken one meter above the ground at each of the 188 sampling sites in February 2014. We processed images to differentiate canopy and sky using ImageJ and calculated percentage canopy cover as 100 times the number of canopy pixels divided by total pixels. In February 1998, hemispherical photos were taken two meters true north from the central point at each site and oriented true north, one meter above the ground using a 35 mm SLR with a fisheye lens. Photos were taken in the period before sunrise or after sunset on calm days so that the canopy was clearly defined. Negatives were digitized and analyzed using *CANOPY* (Ecosystem Dynamics, Research School of Biological Science, Australian National University—I. Noble, I. Davies and T. Montgomery; unpublished, 1985), which traces the path of the sun at 15-min intervals over the scanned image of the vegetation cover and estimates the clear day direct solar radiation from an atmospheric transmission model.

In February 1997 and February-May 2013, ground cover and fallen wood were surveyed at all 188 sample sites. We measured percentage ground cover of leaves, bark, grass, bare ground, rock, wood, moss, and *Lomandra longifolia*. We used a point intercept survey with 10 m transects in five directions (72 degrees apart) from the central point of each site. A 10 m cord was marked every 50 cm and the ground cover (bark, leaves, etc.) that the mark contacted was scored, giving a total of 100 points at each site. Litter depth (cm) was also measured at each mark. By running transects in five directions from a central point, the measures were deliberately biased toward the center of the site, giving greater weight to habitat characteristics close to the pitfall traps.

The quantity of fallen wood at a site was also measured by walking each 10 m transect and scoring all wood under the cord. Fallen wood was scored for five categories with diameters of 1 cm, 2.5 cm, 5 cm, 20 cm, and 40 cm and over. Fallen wood was also scored as rotting (visible substantial deterioration) or intact.

Data analysis

Amphipod data were sparse (consisting of many zeroes) and so were combined into three five-year blocks: 1987–1991 (years 1–5 post fragmentation), 1994–1998 (years 8–12 post fragmentation), and 2010–2014 (years 23–27 post fragmentation). We fitted a generalized linear mixed model (GLMM) for each time period to estimate effects of fragmentation, size, edge, and topography on amphipod abundance. In all models, the response variable was amphipod abundance. We assumed a Poisson distribution and log link for amphipod abundance. The experimental

design is nested, with sampling sites nested within patches, which are nested within replicates. Two random effects, Replicate and Patch, were included in all GLMMs. Four variables were included as fixed effects. (1) Fragmentation: a categorical variable at the replicate scale with two levels (fragments, controls), which tests for the overall effect of fragmentation. (2) Size within fragmentation: a categorical variable at the patch scale with four levels (small, medium, large, control), which tests for the effect of fragment size nested within fragmentation (i.e., the interaction between fragmentation and patch size). (3) Edge within fragmentation: a categorical variable at the site scale with three levels (edge, core, control), which tests for the effect of edge nested within fragmentation (i.e., the interaction between fragmentation and proximity to a fragment edge). (4) Topography: a categorical variable at the site scale with two levels (slope, drain), which accounts for known environmental variation in the understory plant community associated with topography. We included the covariate Log of amphipod abundance (natural logarithm) in the first 2 years of the experiment, before the fragmentation treatment was applied, to account for the spatial variation in the distribution of amphipod abundance before fragmentation. In separate GLMMs, we estimated the effects of the matrix on amphipod abundance for each time period. These models included the fixed effect of Fragmentation, which in this case had three levels (fragments, controls, and matrix), in contrast to the two levels in the analyses above. We used likelihood ratios as the test statistic to calculate p values for each experimental treatment assuming a chi-squared distribution. Effect sizes were calculated as the difference in abundance on the natural logarithm scale between (1) matrix and controls and (2) fragments and controls, respectively.

Finally, we repeated the above analysis in each year, from year 1 through year 27 post fragmentation (excluding years 13–22), to calculate effect sizes in each year for the effect of fragmentation and the effect of the matrix on amphipod abundance. Whereas the analyses described previously required data aggregation across years to examine detailed features of the experimental design (15 parameters), data were sufficient to estimate effects in these simpler models (2 parameters) in each year. We then regressed fragment effect sizes against matrix effect sizes using a linear model to determine whether the amphipod's response

within matrix habitat predicted its response in fragment habitat and to estimate the fragment:matrix logresponse ratio. As these effect sizes are in a temporal series, we explored the potential for temporal autocorrelation by plotting residuals versus time, plotting the partial autocorrelation function, and conducting a Durbin-Watson test (Durbin and Watson 1971).

In a separate GLMM, we examined the relationship between amphipod abundance and environmental variables to determine its realized abiotic niche. We assumed a Poisson distribution with log link for abundance and included the random effects Replicate and Patch. From our broad habitat survey and microclimate data, we selected variables that we hypothesized could potentially explain amphipod distribution and abundance in years 23-27 post fragmentation. These variables grouped into four classes: ground cover and structure, soil properties, canopy cover, and temperature. Using likelihood ratio tests, we found six environmental variables that independently were significantly (P < 0.05) associated with amphipod abundance. We fit a full model containing all six variables plus the random effects, Replicate and Patch. We then used a combination of forward and backward selection to determine a final model composed of environmental variables that predicted amphipod distribution and abundance.

Finally, we used a structural equation model (SEM) to determine the direct and indirect (abiotic) effects of fragmentation on amphipod abundance in years 8-12 after fragmentation and 23-27 after fragmentation. We did not collect abiotic environment data for years 1-5 after fragmentation. We used the piecewiseSEM R package (Lefcheck 2016) and fit linear mixed models to log-transformed amphipod abundance. We only considered data from fragments and controls (excluding matrix data) because we did not collect abiotic data for matrix sites in years 8-12. We considered the direct effects of fragmentation and fragment size, and the indirect effects of canopy cover/radiation. Both models include the random effects of Replicate and Patch. For all analyses described above we used R 3.5.0 (R Core Team 2018).

Results

fragmentation showing instead large declines initially but recovery and even slight increases in abundance in fragments compared to controls in the long term (Fig. 2). Immediately after fragmentation (years 1–5 post-fragmentation), when the matrix was composed of pine seedlings (Fig. 3B), amphipods declined in abundance in fragments compared to continuous forest (Fig. 2A, Table S1; Margules et al. 1994). Notably, during these early years, amphipods almost completely disappeared from the matrix (Fig. 2A, Fig. S2). In fragments, declines in amphipod abundance were greatest in small and medium fragments and at large fragment edges, whereas large fragment cores were less affected (Fig. 2B). Declines in amphipod abundance were more severe in slope habitat compared to drainage lines (Fig. 2C, Table S1).

In years 8–12 post-fragmentation, when the pine trees in the matrix were about 10–15 m high, amphipods continued to be less abundant in fragments than continuous forest overall (Fig. 2A, Table S2). However, this result was driven by small and medium fragments; amphipods were not less abundant in large fragments than continuous forest and edge effects were not apparent (Fig. 2B). Again, amphipods declined most in slope habitat (Fig. 2C).

By years 23–27 post-fragmentation, when the pine trees in the matrix were nearing maturity and overtopped the eucalypt trees in fragments (Fig. 3A), the overall impact of fragmentation on amphipod abundance had disappeared (Fig. 2A–C, Table S3). Indeed, amphipods were more abundant in some fragment treatments than in continuous forest, particularly large fragments and small fragment cores (Fig. 2B). Amphipods were also more abundant in fragment, drainage-line habitat than in continuous forest, drainage-line habitat (Fig. 2C).

We regressed fragment effect sizes against matrix effect sizes to calculate the fragment:matrix logresponse ratio. With the exception of year 1, the relationship of the responses was approximately linear (Fig. 3C). The amphipod's response within matrix habitat predicted its response in fragment habitat, in both the short and long term, with a fragment:matrix log-response ratio (slope) of 0.49 (Fig. 3C; d.f.=1, 4, F-statistic=70.29, P < 0.001, CI 0.37, 0.60). Year 1 was an outlier with high leverage and was not included in the regression. It makes sense to exclude year 1 from the log-response ratio regression because the fragmentation treatment was applied during that



Fig. 2 A Effect sizes, defined as the difference in ln(abundance) of fragments from controls or of matrix from controls. **B** Effect sizes grouped by fragment size and edge/ interior location. **C** Effect sizes grouped by habitat type

year, including clearing trees, burning refuse, and planting pine seedlings. This disturbance would have contributed to the extreme decrease in amphipod abundance in the matrix while the fragment habitat would not yet have had time to fully respond. A partial autocorrelation plot did not reveal significant autocorrelation at any lag value, and a Durbin-Watson test did not reject the null hypothesis of no autocorrelation (P=0.21), suggesting the assumption of independent errors was not strongly violated.

The abiotic niche of amphipods was distinctive, characterized by a shady, moist environment (Fig. 4; Table S4). The variables considered grouped into four classes: ground cover and structure, soil properties, canopy cover, and temperature. Four variables described the amphipod's abiotic niche: amphipods were most abundant in habitat that was dominated by

(slopes, drainage lines). For each period, effect sizes were estimated from a GLMM with log link and Poisson distribution. Error bars are 95% confidence intervals. Photos show the matrix in each period

Lomandra longifolia (P < 0.001, Fig. 4A), had soils with higher pH (P < 0.001, Fig. 4B), and that were moderately wet (P < 0.001, Fig. 4C), and had the greatest tree canopy cover (P < 0.001, Fig. 4D).

The piecewise SEM analyses show how the causal pathways determining amphipod abundance were different in the second and third decades after fragmentation (Fig. 5). In years 8–12 after fragmentation, fragmentation directly had a negative impact on amphipod abundance in medium and large fragments. Fragmentation had a positive impact on total solar radiation, which was statistically significant in medium fragments. In turn, total solar radiation had a negative impact on amphipod abundance. In years 23–28 after fragmentation, when the matrix was mature, fragmentation had a weaker negative impact on amphipod abundance and a strong negative effect



Fig. 3 A Google Earth image of the mature pine plantation matrix and *Eucalypt* fragments 24 years after fragmentation. **B** Aerial photo of the pine seedling matrix and *Eucalypt* fragments 2 years after fragmentation (photo C.R. Margules). **C** Effect sizes in the matrix predict effect sizes in fragments in an approximately linear relationship with a fragment:matrix logresponse ratio (slope) of 0.49. Effect size is the difference in ln(abundance) of fragments from controls or matrix from controls. Numbers are years since habitat fragmentation (colors align with year post fragmentation). The dotted line shows a 1:1 relationship for comparison

on percent cover of sky. In turn, there was a negative relationship between percent cover of sky and amphipod abundance, confirming that amphipods were more abundant at shady sites.

Discussion

The short-term response of the amphipod, *A. sylvaticus*, to experimental fragmentation did not predict its long-term response (Fig. 2). Our result suggests that existing habitat fragmentation research, much of which reports short-term responses or single snapshots in time, may not capture species' long-term trajectories in fragmented landscapes, and especially in landscapes where the matrix is dynamic (McClenahan et al. 2016; Evans et al. 2017; Resasco et al. 2017, 2019; King et al. 2018; Tuff et al. 2019). Ultimately, planning for conservation management based on short-term monitoring of fragmented populations may prove short-sighted.

Instead, over both the short- and long-term, the amphipod's response in fragments was linearly predicted by its response in matrix habitat with a fragment:matrix log-response ratio of about one half. This ratio was quantitatively similar to that found by Evans et al. (2017) for predatory carabids, also in the Wog Wog experiment. When the amphipod declined in abundance in the matrix it also declined in fragments (but less than in the matrix), and when the amphipod increased in abundance in the matrix) (Fig. 3C). Our results provide evidence that the ratio generalizes across the invertebrate food web regardless of trophic position.

We conjectured that abiotic conditions in the matrix would determine the degree of isolation of amphipod populations on fragments and the size of amphipod populations in the matrix, and would also influence the suitability of fragment habitat for amphipods since abiotic conditions in the matrix affect abiotic conditions on fragments. We thus expect fragmentation to affect amphipod abundance in fragments both via isolation and reduced population size, and via changes to fragment habitat according to the match of the amphipod's abiotic niche with abiotic conditions in the matrix over time. The amphipod's realized niche, defined broadly in terms of abiotic conditions (Mac Nally 2000; Kearney and Porter 2009) at Wog Wog sampling sites, was composed of wetter, shadier sites (Fig. 4). Our data suggest that these niche requirements drove the response of the amphipod to fragmentation over 27 years.

In the newly clear-cut matrix, abiotic conditions were extreme relative to the amphipod's niche, with



Fig. 4 Model describing the amphipod's abiotic niche from a Poisson generalized linear model for years 23–27. A Dominant ground cover (Lomand. = Lomandra a dominant tussock-forming plant, error bars are standard errors), **B** Soil pH,

no forest canopy, high solar irradiance, and likely low soil moisture and high desiccation rates. Thus, amphipods all but disappeared from the matrix (Fig. 2A). Amphipods were now also essentially isolated on fragments. Fragments were now surrounded by recently clear-cut forest and therefore became more open to solar irradiance and wind and were therefore likely also drier, thus moving away from the ideal niche of the amphipod. As a result of either isolation on fragments or habitat change on fragments, or both, amphipods steeply declined in abundance in fragments compared to controls. While the decline in fragments mirrored the decline in the matrix it was not as great, leading to logresponse ratios less than one-to-one (Fig. 3C). In accordance with its abiotic niche, declines were greater in slope (dryer) than drainage line (wetter) habitat (Fig. 2C). Furthermore, in the cores of large fragments, where abiotic conditions would

slope=0.18, S.E.=0.01, C Soil wetness (error bars are standard errors), and D Percent tree canopy cover, slope=0.19 S.E.=0.01

have been most buffered from the clear-cut matrix, amphipods did not decline (Fig. 2B).

In years 8–12, with the pine plantation grown to a height of around 10 m and canopy partially closed, abiotic conditions in the matrix moderated when compared to the amphipod's niche, with lower solar irradiance and cooler, moister conditions than immediately following fragmentation. Amphipods showed some recovery in the matrix (Fig. 2A), thereby becoming less isolated on fragments. Abiotic conditions in fragments were now slightly buffered by small pine trees, but solar radiation was still higher in fragments than controls and negatively impacted amphipod abundance (Fig. 5). As a result of either or both reduced isolation and less severe abiotic conditions, amphipod abundance recovered slightly in fragments (Fig. 2A, B), but, again, was lower in the matrix than fragments, leading to log-response ratios less than one-to-one (Fig. 3C).



Fig. 5 Results from a piecewise structural equation model (SEM) showing the relationship between fragmentation, environmental variables, and ln(abundance) of the amphipod *Arcitalitrus sylvaticus* from years 8–12 and 23–27 after fragmentation. Data are for fragment and control sites only (excluding pine matrix sites) because abiotic matrix data were not collected in years 8–12. R^2 values for component models are shown. Black arrows show positive relationships among

By years 23–27 post-fragmentation, trees in the pine matrix were taller than eucalypts in fragments and the matrix canopy had closed, so that matrix habitat had low solar irradiance and cool, moist conditions well matched to the amphipod's abiotic niche. Amphipod populations in the matrix were now similar to controls (Fig. 2A) and fragment populations were no longer isolated. As pine trees overtopped fragments, there was greater canopy cover in fragments than controls (Fig. 5), positively impacting amphipod abundance. As a result of lack of isolation and well-matched abiotic conditions, amphipod abundance was similar across different-sized fragments, edges, interiors, and controls (Fig. 2A, B), and logresponse ratios tended to show larger positive effects in the matrix than fragments (Fig. 3C).

In summary, our data suggest that abiotic niche requirements drove the response of the amphipod to fragmentation over 27 years; however, resource

variables, while red arrows show negative relationships. Where multiple lines are shown, line type indicates fragment size: small (dots), medium (dashes), large (solid). Line thickness is scaled to the magnitude of the standardized regression coefficients, which are shown in boxes on the arrows. Significant pathways (P < 0.05) are opaque, while non-significant pathways are transparent

availability presents an alternate hypothesis, which we briefly consider. The amphipod is a generalist detritivore, feeding on leaf litter in the upper soil layer. Leaf litter in the matrix might have been reduced when the forest was cleared and planted to pine seedlings and then recovered as these trees in the plantation forest matured and shed leaves. However, there was unlikely to have been a loss of leaf litter from the soil in fragments 0–12 years after fragmentation that would explain the reduction in amphipod abundance in fragments, as canopy and soil remained intact.

Increasingly, research in fragmented landscapes illustrates that the matrix ultimately determines the fate of species in fragments (Mesquita et al. 2001; Ricketts 2001; Laurance et al. 2011; Watling et al. 2011; Driscoll et al. 2013; Evans et al. 2017; Resasco et al. 2017; Boesing et al. 2018; Reider et al. 2018). The matrix can provide novel, favored habitat

for fragment-inhabiting species, leading to larger self-sustaining populations in the matrix and the exchange of individuals between the matrix and fragments, increasing the abundances of species in fragments (Davies et al. 2000, 2004; Watling et al. 2011; Driscoll et al. 2013; Evans et al. 2017). Alternatively, if matrix habitat is uninhabitable for a given species, then the matrix can isolate species on fragments, as in the habitat-patch concept (Caughley 1994; Watling et al. 2011; Driscoll et al. 2013; Brudvig et al. 2017), resulting in declines in fragment populations (Davies et al. 2004; Evans et al. 2017; Boesing et al. 2018). The matrix can also alter fragment habitat, changing habitat quality by altering fluxes of wind, water, and solar radiation in fragments (Saunders et al. 1991; Tuff et al. 2016; Reider et al. 2018), which can also positively or negatively impact species there. Finally, if the matrix is dynamic-plantation forestry, agriculture, land under succession or restoration-all of these effects of the matrix can change in time (Evans et al. 2017).

Conclusions

Research from the Wog Wog experiment advances our understanding of the importance of the matrix by illustrating that the response of a species in matrix habitat quantitatively predicts its response in fragments, as shown here for amphipods, and in previous studies of carabid beetles (Davies et al. 2004; Evans et al. 2017). Critically, a fragment:matrix log-response ratio of about 0.5 holds whether a species declined immediately after fragmentation, later increasing in abundance as the pine-plantation matrix matured, as for the amphipod investigated here (Fig. 2), or a species increased in abundance immediately following fragmentation, later declining in abundance as the matrix matured, as for some carabid species reported in Evans et al. (2017). In January 2020, the entire Wog Wog experiment burned in the widespread Black Summer Australian fires. Early evidence shows that the fire burned more intensely in the fragmented landscape than continuous forest (Spiers et al. unpublished data). Future research at Wog Wog should determine whether this ratio persists across taxa as the forest fragments recover and the pine matrix is cleared and replanted. More generally, exploring the generalizability of this log-response ratio in fragmented landscapes globally will be valuable.

Globally, the long-term persistence of forest species depends on their conservation in fragmented landscapes with a dynamic matrix that may only support species during certain periods of management in the matrix. Our findings suggest that management plans must incorporate species' responses in matrix habitat and include projections for favorable and unfavorable periods of matrix dynamics. The presence and abundance of fragment species in the matrix during different matrix management periods might predict whether that species will persist in fragments long term.

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Author contributions MEB and KFD conceived of the study, analyzed data, and wrote the manuscript, AH identified the amphipod and sorted samples with SH, PA, RW and JR. All authors edited the manuscript.

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Data availability Data and R code will be available from the Dryad Digital Repository upon article acceptance.

Code availability No original code was created.

Declarations

Conflict of interest All the authors declared that they have no conflict of interest.

Ethical approval Not applicable.

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