Short- and long-term effects of habitat fragmentation differ but are predicted by response to the matrix

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Running Head: Long-term effects of fragmentation

Abstract

Habitat loss and fragmentation are major threats to biodiversity and ecosystem processes. Our current understanding of the impacts of habitat loss and fragmentation is based largely on studies that focus on either short-term or long-term responses. Short-term responses are often used to predict long-term responses and make management decisions. The lack of studies comparing short- and long-term responses to fragmentation means we do not adequately understand when and how well short-term responses can be extrapolated to predict long-term responses, and when or why they cannot. To address this gap, we used data from one of the world's longest-running fragmentation experiments, The Wog Wog Habitat Fragmentation Experiment. Using data for carabid beetles, we found that responses in the long term (more than 22 years post-fragmentation ~ 22 generations) often contrasted markedly with those in the short term (five years post-

fragmentation). The total abundance of all carabids, species richness and the occurrence of six species declined in the short term in the fragments but increased over the long term. The occurrence of three species declined initially and continued to decline, whilst another species was positively affected initially but decreased in the long term. Species' responses to the matrix that surrounds the fragments strongly predicted both the direction (increase/decline in occurrence) and magnitude of their responses to fragmentation. Additionally, species' responses to the matrix were somewhat predicted by their preferences for different types of native habitat (open vs. shaded). Our study highlights the degree of the matrix's influence in fragmented landscapes, and how this influence can change over time. We urge caution in using short-term responses to forecast long-term responses in cases where the matrix a) impacts species' responses to fragmentation (by isolating them, creating new habitat or altering fragment habitat) and b) is likely to change through time.

Introduction

Habitat loss and fragmentation are significant threats to biodiversity and to ecosystem processes worldwide (McCallum 2007, Stone 2007, Rands et al. 2010, Haddad et al. 2015). There is a long history of ecological research on habitat fragmentation (Fahrig 2003, Didham et al. 2012, Fahrig 2013). Studies that examine either short- or long-term responses to fragmentation are common (e.g. Bell et al. 2001, Collinge and Palmer 2002, Vasconcelos et al. 2006, Thornton et al. 2010, Korfanta et al. 2012, Nijman 2013); however, those that compare and contrast responses between short and long timescales are rare. Addressing this knowledge gap is important because short-term responses are often used to predict long-term responses (Heywood et al. 1994, Tilman et al. 1994, Pimm et al. 1995, Brown et al. 2001, Brook et al. 2003, Hastings 2004, Triantis et al. 2010, Halley et al. 2014).

Theory and the few empirical studies that contrast long- and short-term responses to environmental change suggest that short-term responses rarely, or only weakly, predict long-term responses (Hastings and Caswell 1979, Ovaskainen and Hanski 2002, Briggs and Borer 2005, Hastings 2010, Smith et al. 2010, White et al. 2013). For example, White et al. (2013) showed that the short-term responses of fished species to the establishment of no-take marine reserves did not reflect their responses in the long term. Short-term responses, in which populations remained unchanged, decreased or exhibited single-generation oscillations, were transient and bore no relation to long-term responses. Similarly, in another study, short-term responses to perennial weed invasion did not predict long-term species composition of sown and naturally regenerating swards at agricultural field margins (Smith et al. 2010).

In fragmented systems, there are many possible drivers that might influence different responses in the short and long term. The effects of fragmentation can change over time if there are major changes in the matrix – the environment between the remaining fragments (Driscoll et al. 2013). For example, in an agricultural matrix, the cycles of sowing, maturation, and harvesting of a crop change the structure and resources in the matrix over time (Holland et al. 2005). In particular, natural habitat converted to an agricultural or silvicultural landscape can decrease rates of productivity over multiple crop rotations (Keeves 1966, Kimetu et al. 2008, Tian et al. 2011). This can directly affect the abundance and richness of all species in the crop matrix and therefore fragments embedded in the matrix (Siemann 1998, Mittelbach et al. 2001). Other factors that can change the effects of fragmentation on species over time include population-level effects like crowding (Sharon and Forman 1998, Debinski and Holt 2000, Grez et al. 2004), genetic effects such as genetic drift and inbreeding (Saccheri et al. 1998, Frankham et al. 1999, Higgins and Lynch 2001, Fahrig 2003, Lopez et al. 2009, Bijlsma and Loeschcke 2012), and adaptive responses (Koskinen et al. 2002, Aguilar et al. 2004, Desrochers 2010, Laparie et al. 2010, Hendry et al. 2011, Somervuo et al. 2014), particularly if species are subject to an adaptation lag (Burger and Lynch 1995, Hellmann and Pineda-Krch 2007, Aitken et al. 2008).

Given that most fragmentation studies are snapshots in time, but the effects of fragmentation may change over time, we ask whether short-term observations predict long-term consequences of fragmentation. To address this question, we analyse data from the Wog Wog Habitat Fragmentation Experiment in Australia. The experiment was established in 1985, before fragmentation took place, and offers a rare opportunity to study data collected over a long time scale – from two years prior to fragmentation, until 2011, 22–24 years after fragmentation (Margules 1993, Davies and Margules 1998, Davies et al. 2000, Davies et al. 2001, Davies et al. 2004). Using this data, we asked: how did long-term responses to habitat fragmentation compare with short-term responses for total carabid abundance, carabid species richness and for the 11 most abundant species of carabid beetles; how did long-term responses compare with short-term responses in the matrix surrounding the fragments, and how did these influence responses in fragments of native habitat?

A crucial factor at Wog Wog is that the matrix, a non-native pine plantation, changed considerably over time. Pine seedlings were planted in 1987 but by 2009–2011, the pines were fully mature, reaching a height of over 30 m with a closed canopy that created a shaded understory. The changing matrix may mean that responses in the long term are not of the same magnitude or even direction as in the short term. Pine plantations in Australia can provide suitable habitat for carabid species (Bonham et al. 2002), and studies overseas suggest that this is particularly the case for mature pine plantations (Jukes et al. 2001, Lange et al. 2014). Therefore, we might expect that many of the species will respond positively to the matrix over the long term, which may impact the responses of species to fragmentation. A unique feature of our study is that we examine responses to a changing matrix over time, using data from a spatially and temporally controlled, long-term, landscape scale fragmentation experiment.

Methods

Study site

The Wog Wog Habitat Fragmentation Experiment is located in southeastern New South Wales, Australia (37°04'30''S, 149°28'00''E) in a valley previously covered with open *Eucalyptus* forest. The experiment has a split plot design with six replicates; two replicates are in the control forest and four replicates are in the fragmented forest (Figure 1). Within each replicate there are three square patches, one of each size (0.25 ha, 0.875 ha and 3.062 ha) (Margules 1993). In 1987, the forest surrounding four replicates was cleared and was planted with *Pinus radiata*, leaving remnant patches (here called fragments) of native *Eucalyptus* forest surrounded by a plantation matrix. By 1992, the pines were ~5m in height. The other two replicates in continuous native *Eucalyptus* forest are controls (Figure 1). Each patch contains monitoring sites, stratified by topography into slopes and drainages (termed drains) and by proximity to the edge of the patch (edge or core). Topography primarily affects the understory. Slopes are characterised by tussock grasses, forbs and scattered shrubs, while drains are characterised by dense shrubs of *Kunzea ericoides* and moist areas containing the sedge *Lomandra longifolia* (Austin and Nicholls 1988, Margules 1993). Each of the 18 patches has two replicate sites of the four combinations of edge proximity and topography (core slope, edge slope, core drain, edge drain) (Margules 1993). This gives a total of 144 sites in the *Eucalyptus* forest patches across fragments and controls. Following clearing around the patches, an additional 44 sites were added in the pine matrix in spatially close pairs (one slope, one drain). Two permanent pitfall traps were placed at each sampling site. Traps were opened for seven days, four times a year from 1985 until 1991.

Traps were re-opened in 2009 and sampled three times per year until 2011, repeating the same sampling techniques as the earlier data collections. By 2011 the pines within the plantation were 30 m high. One recent study at the Wog Wog Habitat Fragmentation Experiment showed that small

fragments, as a result of being surrounded by mature pines, are now characterized by increased canopy cover, increased soil moisture, and lower daily maximum temperatures (Farmilo et al. 2013).

Study species

Following on from Davies and Margules (1998), we analysed the effect of fragmentation on the carabid community as a whole using species richness as a response variable. We also focused on the responses of the eight species studied in Davies and Margules (1998) as well as the next three most abundant species. This constituted the eleven most abundant carabid species over the course of the study. These species were *Notonomus resplendens* (Castelnau), *N. variicollis* (Chaudoir), *N. minimus* (Sloane), *N. metallicus* (Sloane), *Eurylychnus blagravei* (Castelnau), *Promecoderus sp.* (Dejean), *Carenum bonelli* (Brulle), *Helluo costatus* (Bonelli), *Hypharpax peronii* (Castelnau), *Amblystomus sp.* and *Scopodes sp.* We added the three latter species, as these species, along with the original eight, were considered abundant enough to offer meaningful analysis (n>40).

Data Analysis

The data were combined into two-year blocks, i.e., 1985-1986 (before fragmentation), and 1987-1989 (short term after fragmentation), 1989-1991 (short-medium term after fragmentation), and 2009-2011 (long term after fragmentation), with each block containing two seven-day samples from each of spring, summer and autumn (Appendix S1: Table S1) allowing for a balanced design of year group factors. As data in years 2009-2011 were collected over three seasons rather than four, we excluded the winter samples from the earlier data so that the earlier data also only represented three seasons.

We used a series of generalized linear mixed models (GLMM) and generalized linear models (GLM) to estimate effects of fragmentation, size, edge, topography and year group. The experimental design is nested, with sites nested within patches, which are nested within replicates. Where possible, *replicate* and *patch* were included in models as random effects, where *patch* was nested within *replicate*. Five variables were included as fixed effects. 1) *Fragmentation*: a categorical variable at the replicate scale with up to three levels (fragments, controls, matrix), which tests for the overall effect of fragmentation. Matrix data were only included in models looking at the effects of the matrix. 2) *Size within fragmentation*: a categorical variable at the patch scale with four levels (small, medium, large, control) which tests for the effect of patch 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 this known environmental variation. 5) *Year group:* a categorical variable with four levels (1985-86, 1987-89, 1989-91 and 2009-2011).

Response variables were carabid abundance, species richness, Chao's estimator of species richness (hereafter referred to as Chao's S) (Chao 1987) and the probability of occurrence of species at sites. We included Chao's S to get a picture of how undetected species might complicate our results. We focused on probability of occurrence rather than abundance for individual species since the data for many species consisted mostly of zeroes and ones with only occasional multiple records per site per time group. Hence, abundance modelling was not feasible for many species and the use of binomial models for all species allowed us to compare effect sizes among species using the same log-odds ratio scale. We fitted separate models for richness and for occurrence of each of the 11 species. We assumed a Poisson distribution for species richness. We first tried GLMMs for all analyses. However, for 10 of 11 species, several treatment combinations had occurrence proportions equal to zero or one, so models including those treatment combinations failed to converge due to the separation

problem (Albert and Anderson 1984). There was no solution to this problem for frequentist GLMMs that was appropriate for these data. Instead, for these species we used penalized likelihood with an ordinary GLM (Firth 1993, Heinze and Schemper 2002), also known as Firth's correction.

Effects of fragmentation on species richness and occurrence of individual species

To estimate the long-term effects of fragmentation, fragment size, edge, and topography, we used a model selection procedure using AICc (Burnham and Anderson 2002) with species richness and individual species occurrence as response variables. As matrix sites do not have attributes of edge and size, it was necessary to exclude the matrix data from this set of analyses. We fitted models with combinations of the interactions of *year group*, *topography*, *fragmentation*, *size within fragmentation*, *and edge within fragmentation*. To answer question 1, two model terms were most relevant: (a) The interaction of *year group* and *fragmentation*, which quantifies how the response to fragmentation changed over the long term compared to the short term; (b) The three-way interactions of *year group*, *fragmentation*, *size within fragmentation*, and *edge within fragmentation*, which quantify how the effects of these treatments changed over time.

To account for spatial autocorrelation within the experiment, we used patch nested within replicate as random effects, except for species where ordinary GLMs were used due to the separation problem. For each species, we ranked all the resulting models, considering those within two AICc (second order Akaike Information Criterion) units of the lowest AICc score (Burnham and Anderson 2002). We tested for remaining spatial autocorrelation using a Moran's I test of the residuals of the top ranked model for species richness and each individual species. Finally, we determined the relative variable importance by summing the Akaike weights of the highest ranked models (ΔAICc<2) that included the given variable or interaction of variables (Burnham and Anderson 2002, Johnson and Omland 2004).

Effects of the matrix on species richness and occurrence of individual species

To investigate the effect of the matrix on long-term carabid responses, we fitted another set of models, this time including all levels of the fragmentation term (fragment, control, matrix) with species richness and the occurrence of individual species as response variables. It was necessary to exclude the data from years one and two, as matrix sites were not included until after fragmentation. To answer question 2, the most relevant model term was the interaction of *year group* and *fragmentation* (including the matrix level), which quantifies how the response to the matrix changed over the long term compared to the short term.

Models were fitted and compared as described above. Where it was possible to use a GLMM to account for spatial autocorrelation, we assigned patch numbers to matrix sites in the spatially close site pairs (within 20 metres of each other) creating an additional 22 patch numbers.

Effect sizes

We calculated effect sizes for the overall effect of fragmentation and the matrix using models only containing the main effects of *fragmentation* (fragments, controls, matrix), *year group* and the *fragmentation-year group* interaction, with all random effects as described above. In these models, we fixed the parameter for the difference between matrix and controls before fragmentation to the difference between fragments and controls before fragmentation (since there were no data for matrix sites before fragmentation). This assumes that the means for matrix habitat before fragmentation were estimated by the means for fragment habitat before fragmentation, which is a suitable assumption since all habitat was the same (native *Eucalyptus* forest) before fragmentation. The fixed parameter was assigned using the offset function in the model formula in R (R Core Team 2016). Confidence intervals for effect sizes were estimated from likelihood profiles.

For abundance, species richness and Chao's S we estimated effect size of fragmentation as the log difference between fragments and controls, subtracting off the observed difference before fragmentation, as follows:

$$(\ln(S_{frag}) - \ln(S_{cont}))_{after} - (\ln(S_{frag}) - \ln(S_{cont}))_{before},$$

where S_{frag} and S_{cont} are abundance, species richness or Chao's S in fragments and controls respectively. Similarly, we estimated effect size of the matrix as the log difference between matrix and controls, subtracting off the observed difference before fragmentation (which was taken to be the same as the difference between fragments and controls before fragmentation, as described above):

$$(\ln(S_{matr}) - \ln(S_{cont}))_{after} - (\ln(S_{frag}) - \ln(S_{cont}))_{before},$$

where S_{matr} is abundance, species richness or Chao's S in the matrix.

For species occurrence, we estimated effect sizes as the log odds ratio of fragments to controls, or log odds ratio of matrix to controls, accounting for the observed ratio before fragmentation, as follows:

$$(\text{logit}(p_{frag}) - \text{logit}(p_{cont}))_{after} - (\text{logit}(p_{frag}) - \text{logit}(p_{cont}))_{before},$$

$$(\text{logit}(p_{matr}) - \text{logit}(p_{cont}))_{after} - (\text{logit}(p_{frag}) - \text{logit}(p_{cont}))_{before},$$

where p_{frag}, p_{cont}, and p_{matr} are the probabilities of occurrence in fragments, controls, and matrix respectively, and the logit function is $\ln(p/(1-p))$.

Analyses and plotting was performed using the 'lme4' (Bates et al. 2016), 'brglm' (Kosmidis 2013), 'vegan' (Oksanen et al. 2016) ,'MuMIn' (Barton 2016) and 'ggplot2' (Wickham 2009) packages in R (R Core Team 2016).

Results

Over the course of the experiment we caught 5017 individual carabid beetles from 45 different species, with the number of occurrences per site within year groups per species ranging from 1 to 463 (Tables S2 and S3).

We detected large and widespread effects of the matrix and of fragmentation on carabid abundance, richness, Chao's S and the odds of occurrence of individual species throughout the time of the experiment (Figure 2). Furthermore, many of the effect sizes shown in the short and short-medium term after fragmentation changed to the opposite sign over the long term. In addition, the responses of species in the matrix were mostly mirrored in the fragments (Figures 2 & 3), indicating the significant effect that the matrix had on species' occurrences within fragments.

Effects of the main treatments (fragments/matrix) on species over time.

The effects of both the matrix and fragmentation changed significantly in time as detected in both the fragmentation and matrix sets of models (Tables 1 & 2). The interaction of year group and fragmentation appeared in the highest ranked models for abundance, species richness, Chao's S and six of the eleven species (Table 1). Similarly, the interaction of year group and the treatments including the matrix (controls/fragments/matrix) appeared in the highest ranked models for abundance, species richness, Chao's S and six species (Table 2).

Effects in the short term

Abundance, species richness and most species were affected to a large extent by both fragmentation and the matrix in the short term (Figure 2), a time not long after clearing and when the matrix consisted of young *Pinus radiata* seedlings. Abundance was strongly negatively affected by both fragmentation and the matrix. Species richness was affected negatively by the matrix by about 25% and by fragmentation by about 20%. Chao's S did not show any effect, possibly indicating that richness in the short term was impacted by undetected species. Ten of the eleven species were

negatively affected by the matrix with nine of these also experiencing very large reductions in occurrence in the Fragments. For example, the odds of occurrence of *Notonomus resplendens*, *Eurylychnus blagravei* and *Amblystomus sp.* in the matrix decreased to around 1/50th, 1/12th and 1/7th of those in the controls respectively. These decreased odds of occurrences in the matrix were accompanied by smaller, but still large, decreases of species' odds of occurrence in fragments (Fig. 2). One species, *Hypharpax peronii*, in contrast to all other species, increased in odds of occurrence in the early matrix by about 150 times its odds of occurrence in controls. Correspondingly, this species also responded positively in fragments, albeit at a smaller positive magnitude than in the matrix and with a large amount of uncertainty as demonstrated by the confidence intervals tending towards infinity (Fig. 2). There is uncertainty associated with these effects of the matrix and fragmentation, as demonstrated by the wide confidence intervals. However, when we examine all effect sizes in the short term together, a general pattern emerges: most species were negatively affected by the young matrix. Furthermore, it is also clear that effect sizes in the matrix were mirrored, to a lesser extent, by effect sizes in fragments (Figures 2 and 3).

Effects in the short-medium term

Over the short-medium term, when pine trees in the matrix ranged from around 2 m to 5 m in height, many of the effect sizes seen in the matrix and fragments, and their directions (positive/negative), were similar to those in the short term (Figure 2). For a number of species, including *Notonomus resplendens*, *N. minimus*, *N. metallicus*, *Eurylychnus blagravei*, *N. variicollis*, *Carenum bonelli* and *Promecoderus sp.*, the reduction in the matrix on species occurrences there had increased over this time. Again, this pattern was echoed by the negative effect of fragmentation on the occurrence of most of these species (excluding *Notonomus metallicus* and *Promecoderus sp.*). *Scopodes sp.* was affected differently than in the short term. This species' odds of occurrence were five times larger in fragment than controls sites, with a corresponding positive, but lesser, increase in odds in the matrix (Figure 2). As with the short-term effect sizes, there is uncertainty in these effect

sizes represented by large confidence intervals. However, again, an overview of all species'
responses reveals a general pattern of mostly similar or increasingly reduced occurrences in the
matrix with paired reductions in the fragments (Figures 2 and 3).

Effects in the long term.

In the long term, when the pines in the matrix had matured and reached a height of 30 metres,
abundance, species richness, Chao's S and many individual species were affected differently than in
the short and short-medium terms (Figure 2). Over the long term, by 2009-2011, and in contrast to
the negative effects shown in the short and short-medium terms, fragmentation and the matrix had
large positive effects on abundance, species richness and Chao's S, with a point estimate
corresponding to about a 50% to 60% increase in all of these metrics per site (Figure 2).
Furthermore, the matrix had a positive effect on the occurrences of *Notonomus resplendens*, *N.
minimus*, *N. metallicus*, *Eurylychnus blagravei* and *Promecoderus sp.* – all species that had shown
negative effects on occurrences in the short and short-medium terms. In addition, many of these
positive effects were very large; for example, *Notonomus minimus* and *N. metallicus* increased in
odds of occurrence in the matrix by roughly 20 and 12 times respectively their occurrence in
controls. *Hypharpax peronii* also showed a contrasting response over the long term with the matrix
affecting its presence negatively as opposed to the positive effects on occurrences in the short term.
Some species, such as *Notonomus variicollis*, *Carenum bonelli*, and *Amblystomus sp.* were not
affected differently over the long term and the short and short-medium terms. There was a similar
pattern of mirrored effects in the fragments and the matrix over the long term as detected in the
earlier time periods (Figures 2 and 3). Again, many of the effect sizes had high uncertainty as shown
by their large confidence intervals. However, the responses of individual species can be clearly
divided between those that were affected by fragmentation and the matrix and those that were not
and the generally large effect sizes offer evidence for biologically important effects for many of the
species.

Effects in the matrix vs effects in the fragments.

Our results revealed a strong over-arching pattern: effect sizes and directions in the matrix determined effect sizes and directions in fragments (slope = 0.44, Figure 3). This relationship spanned all year groups. The resulting linear model of effect sizes in the matrix against effect sizes in the fragments shows that for any given increase or decline in log(odds) of occurrence in the matrix, log(odds) of occurrence in fragments increased or declined by around 44% of the matrix increase or decline.

Effects of topography

Abundance, species richness and Chao's S was greater in drain sites than the slope sites (Appendix S1: Figure S2). Five species preferred drains, whilst one species, *Carenum bonelli*, overwhelmingly preferred slope sites. Three more species, *Scopodes sp.*, *Helluo costatus* and *Promecoderus sp.* preferred slope sites, however the 95% confidence intervals crossed the zero-line indicating uncertainty in this result. The preference of species for drains or slopes determined, for most of the species, how they responded to the matrix over the long term, but not over the short or short-medium terms (Figure 4). For example, of those species that preferred drains, four species responded positively to the matrix over the long term, and the one species that significantly preferred slope sites responded negatively to the matrix over the long term.

Effects of size and edge

Abundance was the only response variable for which the interaction of year group, fragmentation and size appeared in the highest ranked models (Table 1, Appendix S1: Figure S3). However, for all species and overall species richness, the interactions of year group, fragmentation, and edge and of year group, fragmentation, and fragment size did not appear in the highest ranked models (Table 1). There was, however, an interaction of treatment and size (F/S) for species richness and all of the

eleven species (Table 1). This means that, regardless of time, there was a difference in species richness and occurrences between the fragment sizes. These differences carried a large amount of uncertainty with the most reliable patterns being those of species richness, *Eurylychnus blagravei* and *Carenum bonelli*, which showed an increase in the small fragments compared to the controls (Appendix S1: Figure S4). There was also a significant interaction of treatment and edge (F/E) for *Notonomus metallicus* (Table 1). However, inspection of the response plot (Appendix S1: Figure S5) indicates that there was no effect present for this species.

Discussion

Our study of the responses of carabids to fragmentation, using data collected over a timescale longer than in most fragmentation experiments, shows that short-term responses do not necessarily predict long-term effects. Total carabid abundance, species richness, Chao's S and the probability of occurrence for the majority of individual species changed from the short to the long term. These changing temporal responses suggest that short term fragmentation studies (< five years) alone may not be sufficient to understand complex long-term responses of species and communities to fragmentation. Our findings allow us to identify the conditions in which we can have confidence that short-term responses are likely to predict long-term responses, as well as the conditions in which short-term responses are less likely to predict long-term responses.

1) Roles of the matrix: from providing habitat to isolating populations in fragments.

Our findings highlight the importance of the matrix in the responses of species to fragmentation. At Wog Wog, abundance, species richness, Chao's S and the probability of occurrence of six of the species studied showed increases in the matrix over the long term compared to the short and short-medium terms (Figure 2). This indicates that by 2011, the pine matrix had become preferred habitat

for these species. This finding is consistent with other studies showing that pine plantations can provide habitat for some carabid species (Jukes et al. 2001, Bonham et al. 2002, Berndt et al. 2008, Lange et al. 2014).

Whether the matrix becomes suitable habitat seems to depend on the prior habitat requirements of the carabid species in question. Our results show that species associated with *Eucalyptus* forest slope habitats were negatively impacted in the matrix in the long term. Species associated with drain habitats, on the other hand, were positively impacted by the matrix in the long term (Figure 4). This makes sense when we consider that the long-term matrix has a closed canopy and provides habitat more similar to drain sites, which are shadier and moister than slope sites, which are drier and more open. This is consistent with other studies, which have showed that different carabid species respond in positive and negative ways to increased canopy cover (Niemela and Halme 1992, Koivula et al. 1999, Lange et al. 2014).

We detected a strong relationship between the effect sizes in the matrix and the effect sizes in the fragments (Figure 3). This demonstrates that the matrix plays a very large role in determining the responses of species in the fragments. Since the introduction of the theory of island biogeography (MacArthur and Wilson 1967), fragmentation research has, at least in part, conceived of patches as islands in a sea of non-habitat (Fahrig 2003, 2013). This 'habitat patch concept', which discounts the area between patches as totally inhospitable (Fahrig 2003, 2013), is rarely an accurate reflection of the reality (but see Gibson et al. (2013) for a real-world example). Species and community survival within fragmented landscapes is in large part determined by the land type between habitat fragments (Ricketts 2001, Prugh et al. 2008, van Halder et al. 2008, Taki et al. 2010, Driscoll et al. 2013, Sweaney et al. 2014). Our findings confirm this experimentally and demonstrate that at Wog Wog, the matrix is not a "sea" for carabid species. In fact, the long-term changes to the matrix benefit many of the species by providing additional or even preferred habitat. This could be considered to result in a 'species credit' in the landscape (Hanski 2000).

The important role of the matrix can be categorised into four scenarios. In the first scenario, in line with the habitat patch concept, the matrix isolates fragment populations, resulting in declines in fragments (Davies et al. 2001, Davies et al. 2004, Gibson et al. 2013). This scenario applies to many species in the early stages of the Wog Wog experiment when we detected sharp declines in the matrix for species richness and occurrences of nearly all carabid species, accompanied by sharp but smaller declines in fragments. In these early stages after fragmentation, the pine matrix was very young. Vegetation had only recently been cleared and replaced with pine seedlings. This destruction of habitat in the matrix effectively created a 'sea' of non-habitat between the fragments for many species meaning that, at that time, the habitat patch concept applied for those species.

A second scenario, and one that did not appear to be demonstrated at Wog Wog, would be for the matrix to provide supplementary habitat, but not enough to override the negative effects of fragmentation. For example, in the "Biological Dynamics of Forest Fragments Project" (BDFFP) in Brazil, the matrix increased in suitability over the long term, changing from cattle pastures to mosaics of abandoned pasture and secondary regrowth forest (Laurance et al. 2011). This served to lessen the negative effects of the fragmentation in the short term, which advantaged some species, such as insectivorous birds (Stouffer et al. 2009) and dung beetles (Quintero and Roslin 2005); however, effects for most other taxa remained negative (Laurance et al. 2011, Haddad et al. 2015).

In the third scenario, the matrix provides extra resources for species that inhabit fragments (Ewers and Didham 2006), and increases the flow of individuals between fragments (Åberg et al. 1995, Fischer et al. 2006, Mouquet et al. 2006, Davies et al. 2009, Stouffer et al. 2009, Venail et al. 2010, Livingston et al. 2013). In our study, this scenario applies to *Notonomus resplendens, N. metallicus*, *Scopodes sp.* and *Helluo costatus*, which all increased in occurrence in both the fragments and the matrix, but increased more in the fragments than in the matrix (Figure 2).

In the final scenario, the matrix provides new and preferred habitat for species that inhabit fragments, leading to self-sustaining matrix populations (Driscoll et al. 2013) and increasing fragment populations relative to controls (Davies et al. 2001). The responses of *Notonomus minimus, Eurylychnus blagravei* and *Promecoderus sp.* can be interpreted as an example of this scenario. These species show increases in occurrences in both the matrix and the fragments in the long term, with the greatest effect size in the matrix. *Hypharpax peronii* demonstrates this same pattern, but only over the short and short-medium terms.

Our results contrast with experimental evidence to date, which suggests that, for most taxa, fragmentation effects are likely to remain negative in the long term (Haddad et al. 2015). This suggests the responses of species to matrix habitat we observed at Wog Wog might be exceptions, rather than the rule. Nevertheless, our results show that the matrix cannot be assumed to be a sea of non-habitat. Some species may interact with the matrix in more complex ways, especially over the long term.

2) Roles of the matrix: altering fragment habitat

The matrix can also impact populations and communities in fragments by altering fragment habitat (Tuff 2016). For example, we found that most of the species that positively responded to the fragments and the matrix in the long term, preferred drains (Figures 4 and 5), which were cooler and shadier than slope habitat at Wog Wog (Farmilo et al. 2013). Research at Wog Wog has shown that as the pine plantation matured, fragments became cooler than the controls (Tuff 2016). It follows, therefore, that if many of the carabid species prefer habitat that is cool and shady, then their responses to fragmentation may have been driven by the reduction of temperature in the fragments. In contrast, the only species to prefer slope to drain habitat, *Carenum bonelli,* did not

respond positively to the pine matrix in the long term, suggesting that it preferred the younger pine forest because of its preference for more open and drier habitats.

3) The impact of the matrix can change in time

We show that when a matrix changes through time, short-term responses to fragmentation do not predict long-term responses (Figure 2). This is not surprising, given the importance of the matrix in determining species' responses to fragmentation demonstrated above. Abundance, species richness and occurrence of many of the species at Wog Wog had considerably different responses to the fragments and matrix through time. This is as a direct result of the different habitat available in the matrix at different times during the experiment. Most species were negatively impacted in the short term (with one exception) by the removal of habitat and replacement with seedlings. Some of these species recovered to be positively impacted by the fully grown pine plantation over the long term. In the only other long-term study (16 years) carried out in a similar fragmentation experiment within a plantation matrix, the authors predict that effects of pine plantations on birds should increase as the plantation matures (Mortelliti and Lindenmayer 2015). In contrast, our findings suggest that, at least for some carabid beetle species, long-term responses to fragmentation can be the opposite sign to short-term responses (Figure 2).

Conclusion

Our study demonstrates how long-term fragmentation experiments provide critical insights into how species respond to landscape change. We took advantage of one of the longest-running fragmentation experiments to track species' responses over a timescale usually unavailable to ecologists. We showed that long-term responses more than 22 years post-fragmentation can contrast with short-term responses up to five years post-fragmentation. Our findings stress the need

for caution in extrapolating short-term data to predict species' long-term responses to landscape change. In cases where the matrix determines species' responses to fragmentation (by isolating them, creating new habitat or altering fragment habitat), and the matrix is likely to change through time, short-term responses alone should not be used to forecast long-term responses to fragmentation.

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Tables

Table 1. Table showing relative importance of the explanatory variables for the responses of abundance, species richness, Chao's estimator of S and individual species occurrence to the effects of fragmentation. Numbers are based on the sum of the Akaike weights of the highest ranked models (ΔAICc<2) that include the variable (a value of one indicates that the variable appears in all highest ranked models). Variables include year group (Y), fragmentation (F: fragments, controls), topography (T), size within fragmentation (F/S), edge within fragmentation (F/E). Terms separated by a colon indicate interaction terms. Response variables denoted with an asterisk were modelled using a generalized linear mixed model with replicate and patch as a random effect. All other models were generalized linear models using Firth's correction (Firth 1993). See Appendix S1: Table S4 for more detailed results of the model selection.

Response	Y	F	T	Y:F	Y:T	F:T	F/S	F/E	Y:F/S	Y:F:T
Abundance*	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00
Species richness*	1.00	1.00	1.00	1.00	0.40	0.00	0.55	0.00	0.00	0.00
Chao estimator of S*	1.00	1.00	1.00	1.00	1.00	0.41	1.00	0.00	0.00	0.00
Notonomus resplendens	1.00	1.00	1.00	1.00	0.73	0.00	0.50	0.00	0.00	0.00
Notonomus minimus	1.00	1.00	1.00	1.00	1.00	0.00	0.50	0.00	0.00	0.00
Notonomus variicollis	1.00	0.85	1.00	0.55	1.00	0.17	0.42	0.00	0.00	0.00
Eurylychnus blagravei	1.00	1.00	1.00	1.00	0.00	0.00	0.50	0.00	0.00	0.00
Carenum bonelli	1.00	1.00	1.00	0.00	0.00	1.00	0.50	0.00	0.00	0.00
Helluo costatus	1.00	0.76	0.59	0.00	0.00	0.28	0.38	0.00	0.00	0.00
Promecoderus sp.	1.00	0.67	0.30	0.00	0.00	0.00	0.33	0.00	0.00	0.00
Notonomus metallicus	1.00	1.00	1.00	1.00	0.00	0.00	0.50	0.31	0.00	0.00
Hypharpax peronii	1.00	0.67	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00
Amblystomus sp.	1.00	1.00	1.00	0.00	0.00	1.00	0.50	0.00	0.00	0.00
Scopodes sp.	1.00	0.73	0.23	0.19	0.00	0.00	0.36	0.00	0.00	0.00

Table 2. Table showing relative importance of the explanatory variables for the responses of abundance, species richness, Chao's estimator of S and individual species occurrence to the effects of the matrix. Numbers are based on the sum of the Akaike weights of the highest ranked models (ΔAICc<2) that include the variable (a value of one indicates that the variable appears in all highest ranked models). Variables include year group (Y), fragmentation including the matrix (M; matrix, fragments, controls) and topography (T). Terms separated by a colon indicate interaction terms. Response variables denoted with an asterisk were modelled using a generalized linear mixed model with replicate and patch as a random effect. All other models were generalized linear models using Firth's correction (Firth 1993). See Appendix S1: Table S5 for more detailed results of the model selection.

Response	Y	M	T	Y:M	Y:T	M:T
Abundance*	1.00	1.00	1.00	1.00	1.00	1.00
Species richness*	1.00	1.00	1.00	1.00	0.56	0.00
Chao estimator of S*	1.00	1.00	1.00	1.00	1.00	0.31
Notonomus resplendens	1.00	1.00	1.00	1.00	0.32	0.00
Notonomus minimus	1.00	1.00	1.00	1.00	0.00	0.00
*Notonomus variicollis**	1.00	1.00	0.49	1.00	0.29	0.00
Eurylychnus blagravei	1.00	1.00	1.00	1.00	0.00	0.00
Carenum bonelli	1.00	0.65	1.00	0.00	0.00	0.31
Helluo costatus	1.00	0.50	0.00	0.00	0.00	0.00
Promecoderus sp.	1.00	1.00	0.00	1.00	0.00	0.00
Notonomus metallicus	1.00	1.00	1.00	1.00	0.00	0.00
Hypharpax peronii	1.00	0.50	0.43	0.00	0.00	0.00
Amblystomus sp.	1.00	1.00	1.00	0.00	0.00	1.00
Scopodes sp.	1.00	0.50	0.31	0.00	0.00	0.00

Figure legends

Figure 1. Graphic of the experimental site. There are eight sampling sites within each patch, each with two pitfall traps. Paired sampling sites are represented by dots in the pine matrix. Patch sizes are 0.25ha, 0.875ha and 3.062ha. Patches are separated by at least 50m. Note: The eight sampling

sites within each small patch are not represented due to figure space constraints. The location of sites as shown is for illustration only.

Figure 2. Effect sizes for carabid abundance, species richness, Chao's S and individual species occurrence. The effect size is the difference from controls after accounting for the difference before fragmentation on the natural logarithm scale (abundance, species richness, Chao's S) or log odds ratio scale (individual species occurrence). Bars represent 95% confidence intervals. Bars with arrow heads represent confidence intervals tending towards infinity. Where possible, we used generalized linear mixed models to account for random effects. Where separation prevented model convergence, we used Firth's method instead, without random effects (those cases are denoted with an asterisk). Confidence intervals were calculated by profiling. Vertical gray lines represent an effect size of a factor of two on the original scale (i.e. either a doubling or halving of species richness or odds of occurrence).

Figure 3. Plot of effects sizes in the fragments against effect sizes in the matrix for individual species across all of the three post-fragmentation year groups. Effect sizes are as in Figure 2. Colors correspond with species colors shown in Figure 2. Numbers in parenthesis represent the upper and lower 95% confidence intervals. Solid line represents the fitted slope of the relationship. Dotted line represents a 1:1 relationship (slope = 1) with intercept = 0.
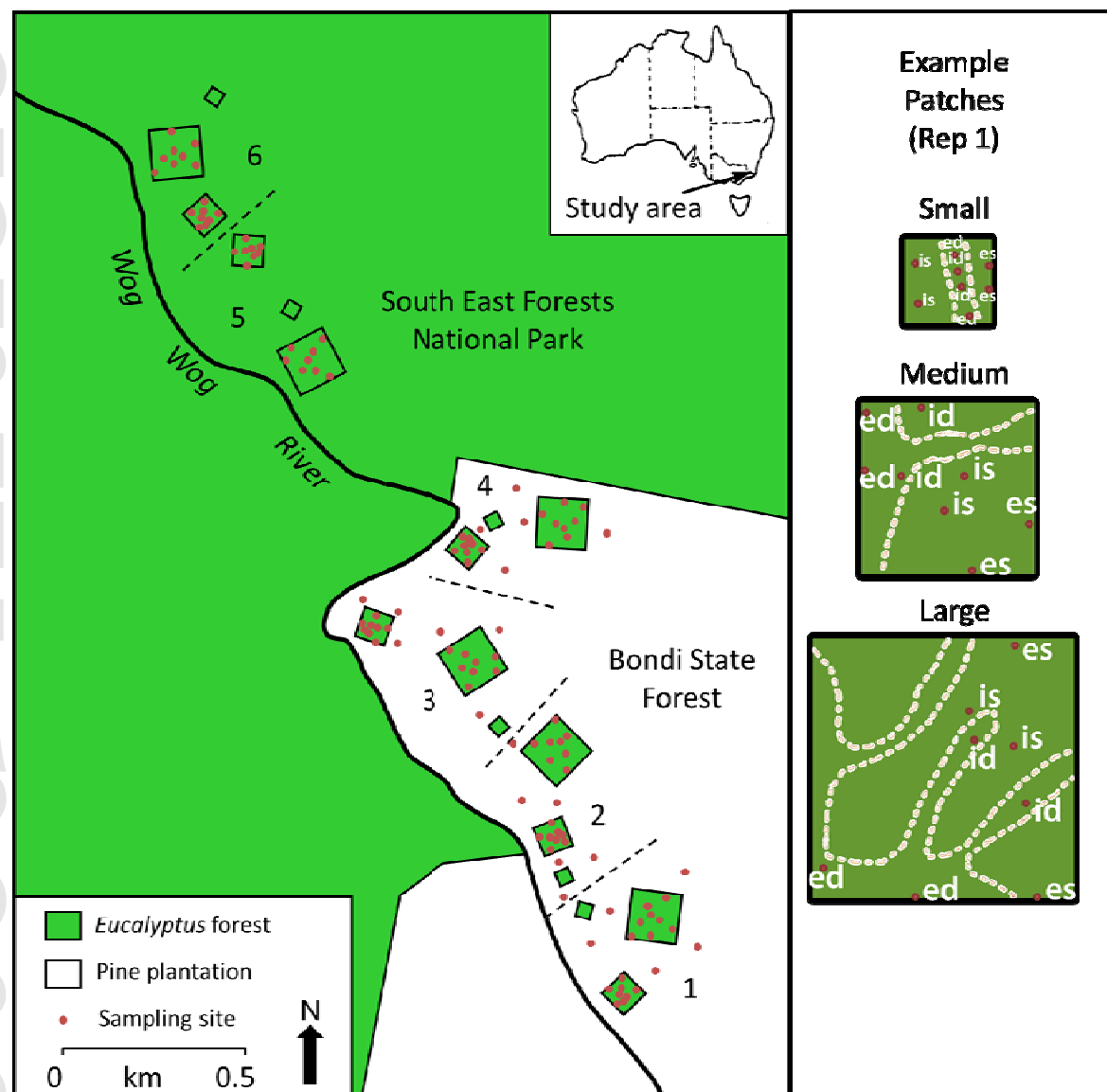
Figure 4. Plot of effect size of topography using fragmentation data only against effect size in the matrix for each individual species in each post-fragmentation year group. Negative effects to topography represent a preference for slope sites, positive effects represent a preference for drain sites. Numbers in parenthesis represent the upper and lower 95% confidence intervals. Solid lines represent the fitted slopes of the relationship. Dotted lines represents a 1:1 relationship (slope = 1) with intercept = 0.
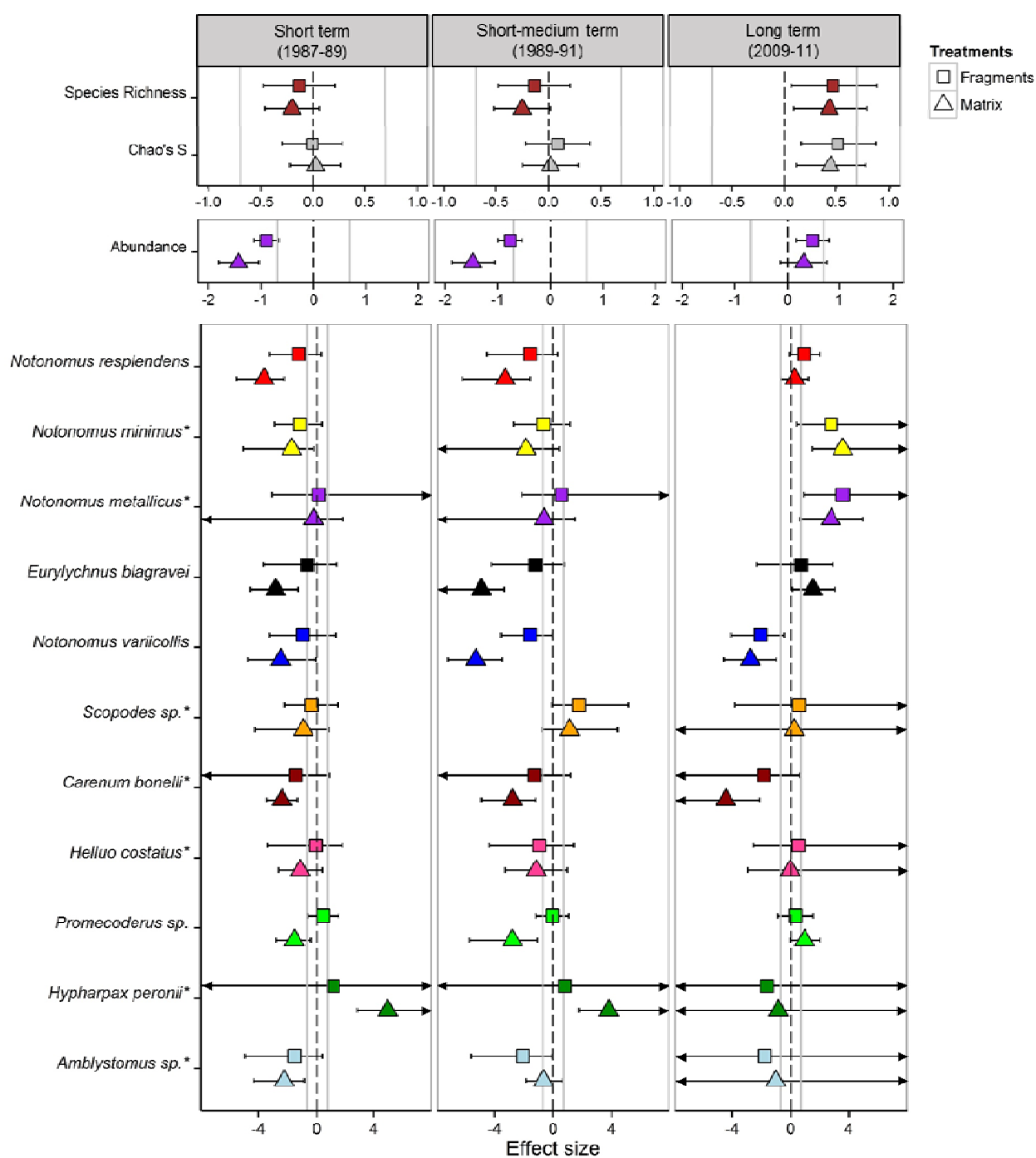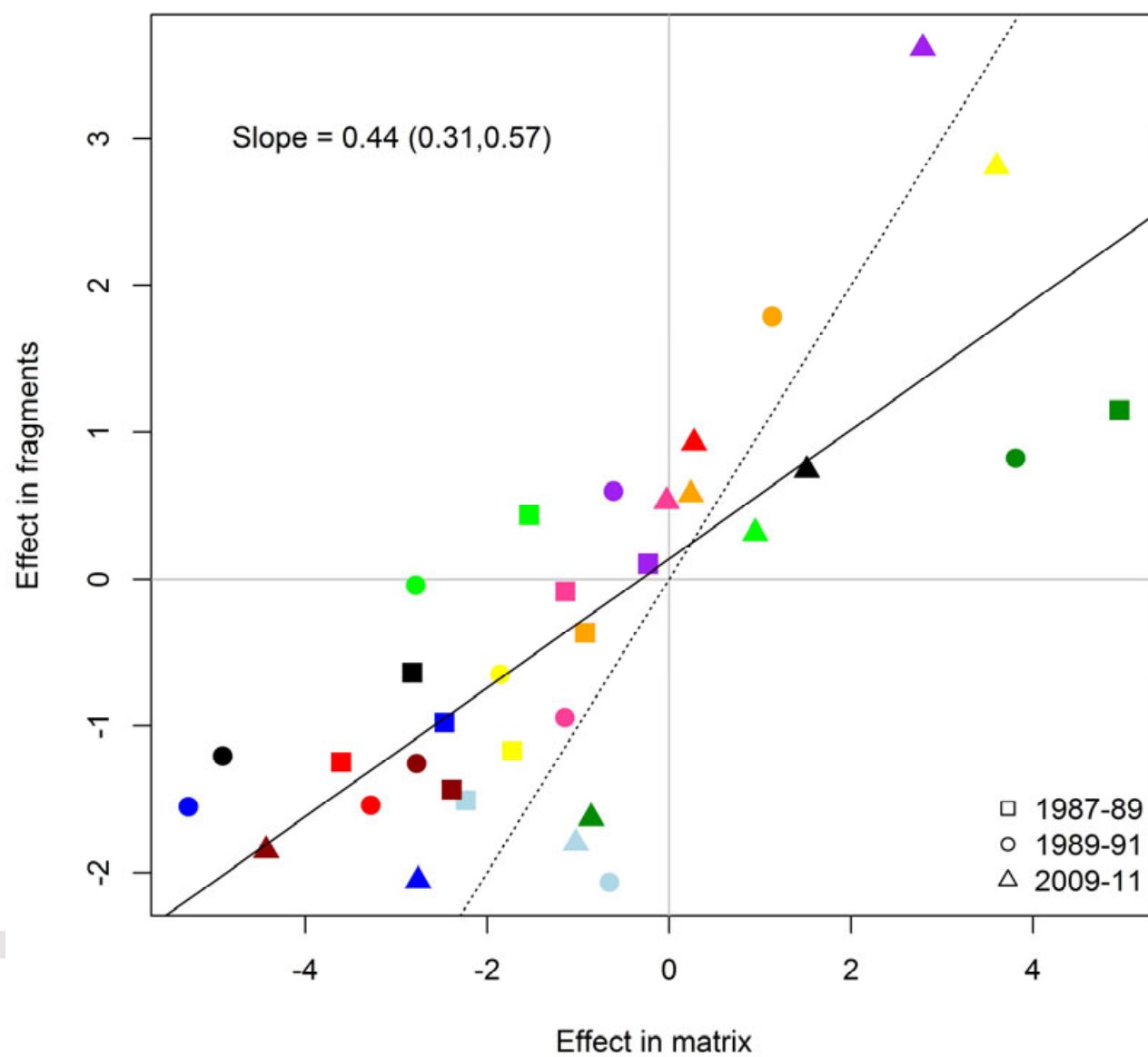
Figure 1.

Figure 2.

Figure 3.

Figure 4.