

A long-term habitat fragmentation experiment leads to morphological change in a species of carabid beetle

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Abstract. 1. Habitat fragmentation and transformation are key drivers of species declines in landscapes. Most of the current understanding of species' responses to environmental change originates from studies of populations and communities. However, phenotypic variation offers another key aspect of species responses and could provide additional insights into the functional drivers of population change.

2. The goal of this study was to address this gap by exploring the morphological changes of a species of carabid beetle (*Notonomus resplendens*) with a known population response to the Wog Wog Habitat Fragmentation Experiment in Australia. We measured morphological traits associated with body size, head width, and dispersal ability. We quantified patterns of morphological variation over time and between native *Eucalyptus* forest fragments and the surrounding pine plantation matrix and the continuous intact native *Eucalyptus* forest controls.

3. We found sexually dimorphic morphological changes in response to the experimental treatments. Males increased in size, had larger legs and had smaller interocular widths in the matrix in both the short and long terms. Conversely, females became comparatively smaller and had increased interocular widths in the same treatments. Effects in the fragments were similar to those in the matrix, but exhibited more uncertainty.

4. Our results demonstrate that species can show morphological change in response to environmental change over very short time periods. We demonstrate that using both population and morphological data allows stronger inferences about the mechanisms behind species responses to environmental change.

Key words. Carabidae, dispersal, fragmentation, long term, morphological trait, Wog Wog experiment.

Introduction

Habitat fragmentation has occurred in landscapes worldwide and has led to widespread changes in biodiversity (McCallum, 2007; Stone, 2007; Rands *et al.*, 2010; Haddad *et al.*, 2015). This has led to an enormous body of literature documenting these changes and synthesising general patterns (Davies &

Margules, 1998; Didham *et al.*, 2012; Fahrig, 2013; Haddad *et al.*, 2015). Yet most of our current understanding of species' responses to environmental change originates from studies of populations and communities (Jackson & Overpeck, 2000; Thomas *et al.*, 2004; Williams *et al.*, 2010). This leaves an important gap in our knowledge of species' responses because many organisms also express phenotypic variation in response to environmental change (Pigliucci, 2001; Norberg & Leimar, 2002; DeWitt & Scheiner, 2004; Miner *et al.*, 2005; Alberti *et al.*, 2017; Moretti *et al.*, 2017). This includes changes in

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behaviour, morphology, growth, life history and demography, which can occur across or even within generations (Black & Dodson, 1990; Black, 1993; Agrawal *et al.*, 1999; Miner *et al.*, 2005). This means that a key aspect of the biology of species is often overlooked when attempting to understand their responses to environmental change.

Morphology is a dominant feature of an organism's phenotype and is directly linked to how it interacts with its environment (Wainwright & Reilly, 1994; Salmon *et al.*, 2014). Investigation of species morphological characteristics, diversity or change can therefore complement knowledge of populations and communities, and yield insight into the factors shaping species' responses to the environment. Habitat change, for example, will affect food quality, vegetation structure, abiotic factors such as temperature, or competition with other species (Kingsolver & Pfennig, 2007; Desrochers, 2010; Laparie *et al.*, 2010; Marnocha *et al.*, 2011). Each of these factors could affect species, and this could be mediated, in part, by how morphology constrains the way individuals within a population interact with their habitat, food, or competitors. For example, a reduction in population density, which increases the amount of food available to remaining individuals, can lead to larger body size of individuals in deer (Ashley *et al.*, 1998). Conversely, a reduction in prey items results in smaller body size of individuals in terns (McLeay *et al.*, 2009). The morphology of species can also involve changes in their shape, independent of their body size, in response to the type of food or resources in new habitat. For example, the relative width of the head of insect species may also constrain their ability to consume larger food items (Pearson & Stemberger, 1980; Laparie *et al.*, 2010).

In addition to the size or shape of organisms, some morphological traits determine how individuals can move or disperse. Typically, better dispersers are more likely to colonise and establish populations in fragmented habitats (Travis & Dytham, 2002; Fahrig, 2003), resulting in selection of individuals with morphological traits that enable better dispersal ability (Travis & Dytham, 2002; Holt, 2003; Desrochers, 2010). This mechanism has been shown in carabids (Laparie *et al.*, 2013), butterflies (Hill *et al.*, 1999) and damselflies (Anholt, 1990).

Research that examines morphological changes within species in response to landscape change and over time is rare (but see Schmidt & Jensen, 2003; Desrochers, 2010; Marnocha *et al.*, 2011). One of the reasons for this is that there are very few long-term studies globally that have sufficient data. This limits our ability to ask questions about long-term phenomena, such as species' responses to long-term landscape transformation and climate change. Here, we quantify the effects of anthropogenic landscape modification on the intraspecific morphology of the carabid beetle species *Notonomus resplendens* (Castelnau, 1867). We do this by using the 25-year-old Wog Wog Habitat Fragmentation Experiment, one of the longest running fragmentation experiments in the world (Margules, 1992; Davies & Margules, 2000; Farmilo *et al.*, 2014; Haddad *et al.*, 2015). The experimental landscape consists of native *Eucalyptus* forest, which was fragmented into experimental remnant eucalypt fragments, with the cleared part of the landscape replaced with *Pinus radiata* plantation forest.

The overarching question addressed in this study is: does the landscape change at Wog Wog lead to morphological changes in a species of carabid beetle? We used adult beetles sampled between 1985 and 2013, and measured key aspects of their morphology linked to body size, body shape, and dispersal ability across the fragmentation treatments. We quantified patterns of morphological variation over time, and tested for differences between individuals from remnant native *Eucalyptus* forest fragments (*fragments*) and the surrounding pine plantation matrix (*matrix*) to the continuous intact native *Eucalyptus* forest (*controls*).

The carabid species we selected for study [*N. resplendens* (Castelnau, 1867)] has a known response to the fragmentation over the history of the experiment (Evans *et al.*, 2017). This allowed us to make a number of predictions on how individuals might change morphologically to the landscape change based on the corresponding population responses. Further, using morphological responses in conjunction with the known population responses could allow us to gain a greater understanding of the underlying mechanism behind the population responses to the landscape changes. The species was previously shown to have declined in population in the fragments at Wog Wog in the 2–6 years postfragmentation, but to have increased in population over the long term (22 years postfragmentation) (Evans *et al.*, 2017). This population response in the remnant vegetation fragments is thought to be a result of the effects of the maturing pine plantation matrix, and associated changes in habitat and food resources, over this time (Evans *et al.*, 2017). Given these previous findings, we made four predictions about morphological responses. First, we predicted that this species would show changes in *body size*, as other studies indicate that body size is one of the main traits to respond to environmental variation and landscape change (Laparie *et al.*, 2010; Laparie *et al.*, 2013). Second, we predicted that the species would show morphological changes related to *dispersal ability* in response to new habitat provided by the pine plantation (Laparie *et al.*, 2013). Third, we considered that the species would change its diet in response to the new food resources provided by pine plantations, and so predicted that this species would change its relative *head width* in response to different food items (Pearson & Stemberger, 1980; Laparie *et al.*, 2010). Fourth, we were able to discriminate females from males for individuals of this species, and predicted that *reproductive* potential would change in female individuals of the species.

A key finding in Evans *et al.* (2017) was that population responses in the matrix predicted those in the fragments. This demonstrated that the matrix had a very large impact on the populations in the fragments. We also predicted, therefore, that morphological responses in the matrix would be reflected in the fragments. This would add further evidence to the importance of the matrix and might imply that populations are continuous in the disturbed landscape at Wog Wog.

We compared the morphological responses of this species in light of our predictions, as well as its known population changes (Evans *et al.*, 2017). Our study provides some of the first evidence of the effects of long-term habitat fragmentation on insect morphology.

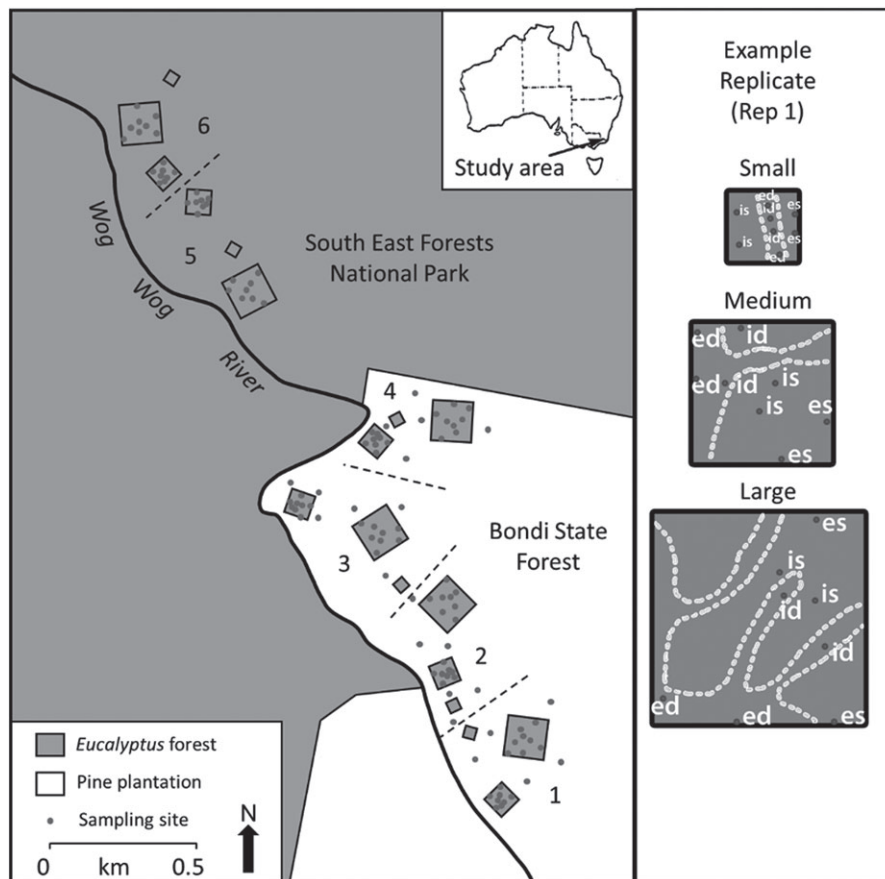


Fig. 1. Map of the experimental site. There are eight sampling sites within each plot, each with two pitfall traps. Paired sampling sites are represented by dots in the pine plantation. Plot sizes are 0.25, 0.875, and 3.062 ha. Plots are separated by at least 50 m. Note: the eight monitoring sites within each small plot are not represented due to figure space constraints.

Materials and methods

Study site

Our study was conducted at the Wog Wog Habitat Fragmentation Experiment (Margules, 1992), which is a long-term and landscape-scale experiment (Davies & Margules, 2000). Located in south-eastern New South Wales, Australia (37°04'30"S, 149°28'00"E), the experiment was established in 1985 (Margules, 1993) in a valley previously covered with open *Eucalyptus* forest. It consists of six replicates of square plots of three different sizes (0.25, 0.875, and 3.062 ha) (Margules, 1993). Each plot contains a number of monitoring sites, stratified by topography into slopes and drains and by proximity to the edge of the plot (edge or interior). Each of the 18 plots was divided into four combinations (interior slope, edge slope, interior drain, edge drain) (Margules, 1993) and replicated twice, giving a total of 144 sites. For example, a site on a slope towards the centre of one of the square plots would be classified as 'interior slope', and a site in a drain on the edge would be classified as 'edge drain'. In 1987, the forest surrounding four of these replicates was cleared and planted with a plantation of *P. radiata* (Fig. 1), often referred to as the matrix. The sites

within these four plots are classified as fragment sites and form the first main treatment of the experiment. Following clearing around the plots in 1987, an additional 44 matrix sites were added in the pine plantation to form the second main treatment of the experiment. The remaining sites in the plots of the two uncleared replicates form the main spatial controls of the experiment. Each site contains two permanent pitfall traps which were opened for 7 days, four times a year from 1985 until 1992. Traps were reopened in 2009 and sampled three times per year until 2013, by which time the pines within the plantation were approximately 30 m high. Throughout the history of the experiment, a subset of the adult beetles were pinned and stored at the Australian National Insect Collection in Canberra, Australia. The temperature near Wog Wog rose from 1991 to 2013, with 2010 being a particularly warm year. Throughout the time of the experiment rainfall fluctuated, with 2008 and 2009 being particularly dry years (Bureau of Meteorology 2017).

Study species

We chose a species of common carabid beetle with a known population response to the experiment: *Notonomus resplendens*

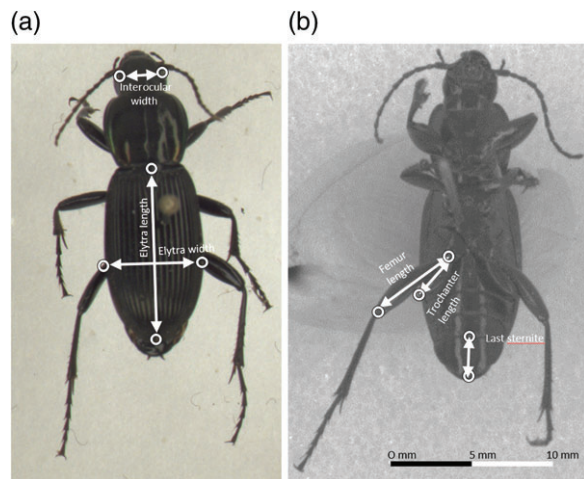


Fig. 2. Examples of images of the dorsal (a) and ventral (b) view of *Notonomus resplendens*, including landmarks as hollow circles and linear measurements as arrows. [Colour figure can be viewed at wileyonlinelibrary.com].

(Evans *et al.*, 2017). Species of *Notonomus* are common to coastal and dry sclerophyll forests of eastern Australia (Mathews, 1987; Lawrence & Slipinski, 2013). *Notonomus resplendens* is a large (18–21 mm), flightless species and is one of the most commonly caught species at the Wog Wog Habitat Fragmentation Experiment. *Notonomus resplendens* is a suitable size for morphological work given the equipment available for this study, and was also available in large enough numbers throughout the time span of the experiment to offer sufficient replication of data for analysis. We investigated using other species of carabid with known population responses to the experiment. However, other species were not available in large enough numbers and were not spread across the treatments adequately enough to be included in the study. We included samples from 1985 to 1987 (pre-fragmentation), 1988 to 1992 (short-term post-fragmentation) and 2009 to 2013 (long-term post-fragmentation).

Measurements

We made morphological measurements using images taken with a SmartDrive SatScan Collections v2.0.10 scanner at the Australian National Insect Collection. Digital landmarks were placed on each image using the software programs TPSUTIL (Rohlf, 2013a) and TPSDIG (Rohlf, 2013b) (Fig. 2). We then used the coordinates of the landmarks to calculate the linear distance between the landmarks. We took linear measurements on each individual beetle (Fig. 2), and split our trait measurements into four categories used to address our predictions, related to body size, head width, dispersal ability, and reproduction.

Body size. As a proxy for overall size, we measured elytra length. We chose the elytra length as opposed to body length for this index, to minimise variation due to orientation or as a result

of parts of the body, such as the head, protruding more in some individuals than others (Smith *et al.*, 2000; Craig Stillwell *et al.*, 2007).

Dispersal ability. To obtain a metric relevant to dispersal capacity, we measured femur length and metatrochanter length. Leg length is considered to indicate dispersal ability (Laparie *et al.*, 2013). We measured metatrochanter length because carabid species that run typically have longer trochanters than do species that use pushing to move through their environment (Evans, 1977).

Head width. We measured the distance between the eyes (fore interocular width) as a proxy for head width (Laparie *et al.*, 2010). This allowed us to examine whether the beetles had responded to different food items that require a smaller or larger head width to consume food effectively.

Reproduction. We measured the last abdominal sternite, a trait that has been shown to be larger in females than in males in carabids and is thought to indicate greater female fecundity in new habitats (Laparie *et al.*, 2010).

Data analysis

As size is the dominant morphological trait among animals (Peters, 1983), we needed to account for the patterns of variation in other morphological traits beyond that which is correlated with body size (Barton *et al.*, 2011). We therefore used elytra length as a covariate in all models, apart from when we analysed elytra length itself as a response variable.

All our statistical analyses of beetle morphological responses to time and experimental treatments (fragments, matrix) were conducted using linear mixed effects models with the ‘lme4’ (Bates *et al.*, 2016) and ‘MuMIn’ (Barton, 2016) packages in R (R Core Team, 2017). We assumed a Gaussian distribution and tested this assumption by checking for normally distributed residual errors, and accounted for potential spatial autocorrelation in our data for all models by fitting patch nested within replicate as random effects in the models.

Our fixed effects comprised time, the experimental treatments, and the sex of the beetle. To test for the effect of time, we combined our morphological data into year blocks, defined by 1985–1987 (pre-fragmentation), 1988–1992 (short-term post-fragmentation) and 2009–2013 (long-term post-fragmentation). Pine plantation sites were not established until after fragmentation, meaning we did not have a balanced design of all time \times treatment combinations. We therefore subsetted our data to reflect this, resulting in two kinds of models (model set no. 1 and model set no. 2, respectively) (see Table S1).

Model set no. 1 – all time periods but excluding pine plantations. We tested whether there was an effect of time

Table 1. Summary of full models used for variable selection using second-order Akaike information criterion model ranking.

Data used	Full model
Pre-fragmentation (model set no. 1)	Morphological trait $\sim Y + F + T + Y \times F + Y \times F/S +$ $Y \times F/E + Y \times T + F \times T + Y \times F \times T +$ $Y \times \text{Sex} + F \times \text{Sex} + T \times \text{Sex} +$ $Y \times F \times \text{Sex} + Y \times F/S \times \text{Sex} +$ $Y \times F/E \times \text{Sex} + Y \times T \times \text{Sex} +$ $F \times T \times \text{Sex} + Y \times F \times T \times \text{Sex}$
Plantation matrix (model set no. 2)	Morphological trait $\sim Y + F + T + Y \times F + Y \times T + F \times T +$ $Y \times F \times T + Y \times \text{Sex} + F \times \text{Sex} +$ $T \times \text{Sex} + Y \times F \times \text{Sex} + Y \times T \times \text{Sex} +$ $F \times T \times \text{Sex} + Y \times F \times T \times \text{Sex}$

Y, year group; F, main treatments; T, topography; S, size; E, edge; \times , interaction + variables alone (e.g. $Y \times F$, $Y + F + Y:F$); /, nested interaction.

($R[\text{morphological trait}] \sim Y[\text{year block}]$) or if there was an interactive effect of time and treatment ($R \sim Y \times F[\text{treatment of controls versus fragments}]$). We also tested for effects of the nested treatments of fragment size ($R \sim Y \times F/S[\text{size}]$) and edge ($R \sim Y \times F/E[\text{edge}]$) and for effects of topography (i.e. slopes and drainage lines) ($R \sim T[\text{topography}]$), its interaction with year group ($R \sim Y \times T$), treatments ($R \sim F \times T$) and the further interaction of time ($R \sim Y \times F \times T$). We also included sex as an interacting factor in the models (See Table 1 for full models). We ranked all the resulting models, including the null model, considering those within two second-order Akaike information criterion (AICc) units of the lowest AICc score (Burnham & Anderson, 2002). Finally, we determined the relative importance of the predictor variables by summing the Akaike weights of the highest ranked models ($\Delta\text{AICc} < 2$) that included the given variable or interaction of variables (Burnham & Anderson, 2002; Johnson & Omland, 2004).

Model set no. 2 – two time periods but including all experimental treatments. For the data that included the pine plantation sites, we repeated the same model selection procedure as the models with the pre-fragmentation data; however, we excluded the nested treatments of size and edge (Table 1).

Effect sizes

To understand the direction and relative magnitude of beetle trait responses to the treatments of fragment and matrix, we calculated effect sizes using linear models of our response variables against the main treatments (eucalypt fragments, eucalypt controls, pine plantation matrix), time (3-year blocks), and their interactions. As with our model selection procedure, we used patch nested with replicate as random effects. Because there were no data for the matrix sites before fragmentation took place, we fixed the parameter for the difference between the matrix and controls before fragmentation to the difference between the fragments and controls before fragmentation. This assumption is suitable because the habitat in the matrix before fragmentation was the same as the habitat in the fragments (i.e. native *Eucalyptus* forest). This parameter was assigned using the offset function in the linear model formula in R (R Core Team,

2017). Effect sizes for fragments were the difference between the fragments and controls at each year block after the observed difference between the fragments and controls before fragmentation was subtracted, as follows:

$$(R_{\text{frag}} - R_{\text{cont}})_{\text{after}} - (R_{\text{frag}} - R_{\text{cont}})_{\text{before}}$$

where R_{frag} and R_{cont} are the observed means of trait response variable in the fragments and controls, respectively. Effect sizes for the matrix sites were the difference between the matrix and controls at each year block after the observed difference between the fragments and controls before fragmentation was subtracted:

$$(R_{\text{matrix}} - R_{\text{cont}})_{\text{after}} - (R_{\text{frag}} - R_{\text{cont}})_{\text{before}}$$

where R_{matrix} is the observed mean of the trait response variable.

We calculated the effect sizes for both males and females, by subsetting the data before running the models. We estimated confidence intervals (CIs) for the effect sizes from likelihood profiles.

Plotting was performed using the 'ggplot2' (Wickham, 2009) package in R (R Core Team 2017).

Results

We measured 374 individuals of *N. resplendens* (Table S1).

Morphological responses to the fragments and matrix after fragmentation

Notonomus resplendens changed morphologically over time, indicated by year block appearing as an important predictor variable for all of the morphological traits in both sets of models (Tables 2 and 3). Changes in elytra width (model no. 1) and in trochanter and femur length (model no. 2) were also explained by an interaction between year block and the main treatments relating to habitat fragmentation.

The plotted effect sizes revealed a mix of positive and negative responses of morphological traits of *N. resplendens* in response to the fragments and matrix, over time, and between males and females (Fig. 3).

Table 2. Results of second-order Akaike information criterion (ΔAICc) model selection for model set no. 1 for *Notonomus resplendens*.

Response	Y	F	T	Sex	Y × F	Y × Sex	T × Sex	F × Sex	Y × T	Y × T × Sex
Elytra length	1.00	0.27	–	1.00	–	0.24	–	–	–	–
Elytra width	1.00	0.49	–	–	0.27	–	–	–	–	–
Femur length	1.00	0.27	0.21	1.00	–	1.00	–	–	–	–
Trochanter length	1.00	0.33	–	1.00	–	1.00	–	–	–	–
Interocular width	1.00	0.46	0.14	1.00	0.14	0.89	–	0.34	–	–
Last sternite	1.00	0.19	0.34	1.00	–	0.30	0.13	–	0.13	0.13

Table showing relative importance of predictor variables for responses of morphological variables of *N. resplendens* to the effects of year block (Y), treatments (F), topography (T) and sex and a selection of their interactions. Predictor variables that did not appear in the top ranked models are not included in the table (e.g. size, edge). Numbers are based on the sum of the Akaike weights of the highest ranked models ($\Delta\text{AICc} < 2$) that include the variable (a value of 1 indicates that the variable appears in all highest ranked models). Terms separated by '×' indicate interaction terms. See Table S1 for more details.

Table 3. Results of second-order Akaike information criterion (ΔAICc) model selection for model set no. 2 for *Notonomus resplendens*.

Response	Y	F	T	Sex	Y × F	T × Sex	F × Sex	Y × Sex	F × T	Y × T	Y × T × Sex
Elytra length	–	–	–	1.00	–	–	–	–	–	–	–
Elytra width	1.00	1.00	0.40	–	–	–	–	–	–	–	–
Femur length	1.00	0.67	–	1.00	0.67	–	–	0.20	–	–	–
Trochanter length	1.00	0.31	–	1.00	0.31	–	–	0.79	–	–	–
Interocular width	1.00	1.00	1.00	1.00	–	0.32	1.00	1.00	1.00	–	–
Last sternite	1.00	–	1.00	1.00	–	1.00	–	1.00	–	1.00	1.00

Table showing relative importance of predictor variables for responses of *N. resplendens* to the effects of year block (Y), treatments (F), topography (T) and sex, and a selection of their interactions. Numbers are based on the sum of the Akaike weights of the highest ranked models ($\Delta\text{AICc} < 2$) that include the variable (a value of 1 indicates that the variable appears in all highest ranked models). Terms separated by '×' indicate interaction terms. See Table S1 for more details.

Body size

Males of *N. resplendens* became bigger in the matrix in the long term, with a strong increase in the short term (Fig. 3). Males did not change in the fragments, as indicated by the very large 95% CIs for effects on elytra length in the fragments (Fig. 3). Females, in contrast, became smaller in the matrix over the short and long terms, but again, did not change in the fragments (Fig. 3). There was a pattern of females becoming more robust in the matrix and fragments of the short and long terms, as shown by an increase in relative elytra width in these treatments. However, the 95% CIs crossing the zero-effect line indicate that there is uncertainty in this response.

Dispersal ability

Femur length and trochanter length showed relative increases for males in the matrix sites over the short and long terms, whilst for females, femur and trochanter length showed a relative decrease over the short term but not over the long term. A similar pattern was shown in the fragments; however, again there was uncertainty in this response as shown by the 95% CIs crossing the zero-effect line (Fig. 3).

Head width

Changes in relative interocular width were strong in the matrix, with males affected negatively and females positively.

This pattern was mirrored in the fragments for females, but not for males (Fig. 3).

Reproduction

In the short term, last sternite length showed a similar pattern to the changes in femur and trochanter lengths; however, only the effect for males in the matrix showed an effect, with 95% CIs that did not cross the zero-effect line. Over the long term, only effects for females in the matrix were positive and with acceptable uncertainty (Fig. 3).

Effects of the matrix versus effects of the fragments for both species

Our results revealed a very strong relationship between effect sizes in the matrix and effect sizes in the fragments (slope = 0.66, $P = 4.00\text{e}^{-9}$, $R^2 = 0.80$). (Fig. 4). This relationship spanned both year groups.

Discussion

We showed that landscape change had, indeed, led to morphological changes in the focal carabid beetle species of our study. The temporally and spatially controlled landscape experiment at Wog Wog allowed us to gain novel insights into how this species has changed morphologically in response to habitat

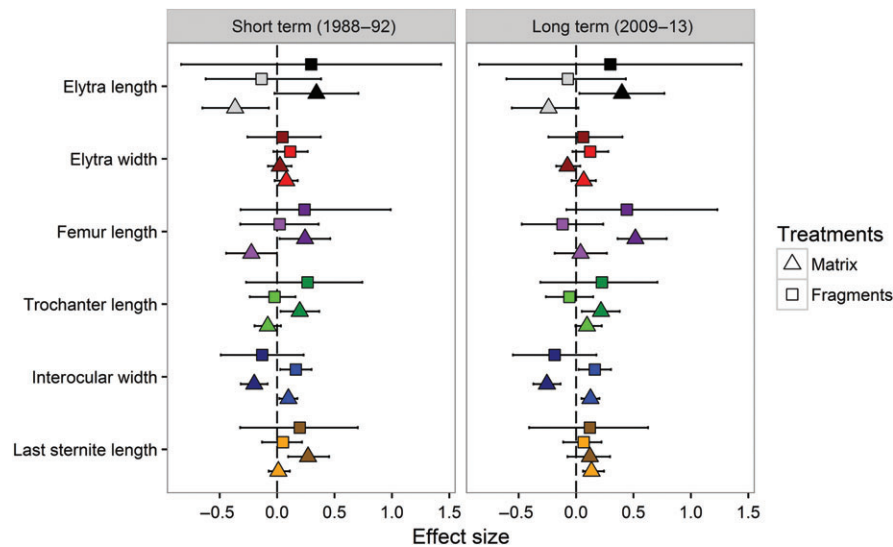


Fig. 3. Effects on *Notonomus resplendens* morphology of the interaction of time and treatment. Effect sizes for each trait are filled with the same colour but have been shaded darker for males and lighter for females (e.g. male elytra width is dark red, female elytra width is light red). Bars represent 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com].

fragmentation. We discuss our findings in the context of the corresponding population response shown by Evans *et al.* (2017). Using both population and morphological data of this species allows us to make stronger inferences about the mechanisms behind its responses to the experimental treatments.

New habitat promotes dispersal related traits

The most compelling morphological responses expressed were related to dispersal, such as changes in femur length and trochanter length (Fig. 3). Most notable were the sexually dimorphic changes in response to the treatments. A key finding in Evans *et al.* (2017) was that this species' population was negatively impacted by the matrix in the short term. In the short term, the early pine matrix was very young, with most vegetation recently cleared and replaced with pine seedlings. At this time, as Evans *et al.* (2017) discuss, the matrix might be considered less preferable than native *Eucalyptus* forest to this species. This would have the result that the landscape, in particular the matrix, would have an insufficient amount of habitat to sustain the populations – a mechanism that is linked to pressures for individuals to emigrate (Schtickzelle & Baguette, 2003; Heidinger *et al.*, 2010). This pressure to emigrate from habitat within the landscape may have led to promotion of dispersal-associated traits for *N. resplendens*, a phenomenon known to occur at invasion fronts for carabids (Laparie *et al.*, 2013) and other taxa (Phillips *et al.*, 2006; Heidinger *et al.*, 2010; Weiss-Lehman *et al.*, 2017). The fact that this selection pressure for increased dispersal-related traits is shown only in males of this species does not invalidate this interpretation. Many species, including carabids (see Lagisz *et al.*, 2010; Laparie *et al.*, 2013), also exhibit sex-biased morphological changes related to dispersal (Travis & Dytham, 2002; Dubois *et al.*, 2010; Heidinger *et al.*, 2010; Tanahashi, 2014), with the

cause thought to be that increased dispersal ability is often offset by lower reproductive rates in females (Crawley, 1989). Furthermore, direct data from at least one species of carabid have shown that males demonstrate more locomotive activity than do females (Szyszko *et al.*, 2004).

In contrast to its population response (Evans *et al.*, 2017), the morphological response of *N. resplendens* remained similar (but possibly increased in effect) from the short to the long term. In the long term, this species increased in occurrence in the fragments and matrix to a point that the matrix could be considered as much as habitat as the native fragments (Evans *et al.*, 2017). As Evans *et al.* (2017) discuss, this was because the pine matrix had changed considerably as the pines grew into mature trees, providing a more similar habitat to that of the *Eucalyptus* forest than previously. At Wog Wog, *N. resplendens* prefers the darker and moister microhabitat of drainage lines to drier and sunnier slopes (Evans *et al.*, 2017). The mature pine plantation in 2009–2013, with its tall and closed canopy, provides cooler, darker habitat than the younger, more open, plantation in the early years of the experiment. The similar morphological responses in the long and short terms might indicate that the mature matrix still exerted selection pressures for increased dispersal over the long term. It is possible that the populations are still adjusting to this new environment and are still dispersing into new habitat. It might also be possible that the differing floor structure of the pine plantation is selecting for dispersal-related traits. The pine plantation floor is a much less complex environment when compared with the eucalypt forest floor. In ants, a decrease in leg length is associated with a more complex habitat (Parr *et al.*, 2003; Farji-Brener *et al.*, 2004; Sarty *et al.*, 2006; Gibb & Parr, 2010; Wiescher *et al.*, 2012). If this were the case with carabids, then we might expect that a simpler habitat structure, such as the pine forest floor, would drive an increase in leg length.

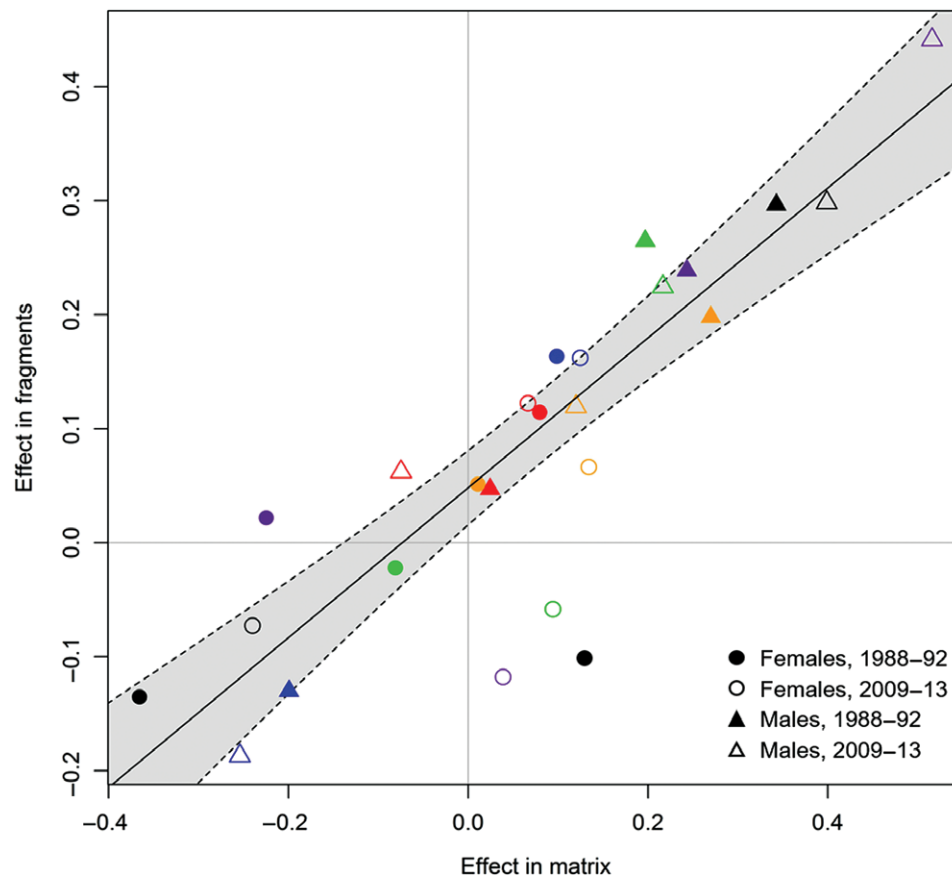


Fig. 4. Plot of effect sizes in the fragments against effect sizes in the matrix for individual traits across both post-fragmentation year groups (slope = 0.66, $P = 4.00 \times 10^{-9}$, $R^2 = 0.80$). Filled points represent 1988–1992 effects and unfilled points represent 2009–2013 effect sizes. Effect sizes are as in Fig. 3. Colours correspond with species trait colours shown in Fig. 3. The solid line represents the fitted slope of the relationship, with the grey area representing the 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com].

Other factors influencing body size sexual dimorphism

Body size in insects is also often directly affected by environmental conditions, especially those experienced during larval development (Margarf *et al.*, 2003; Davidowitz *et al.*, 2004; Lagisz, 2008; Chown & Gaston, 2010; Sukhodolskaya & Ereemeeva, 2013). At Wog Wog, we see a comparative reduction in the size of females in tandem with an increase in the size of males. It may be possible, therefore, that two pressures are manifested morphologically differently in each of the sexes – i.e. that females respond to the poorer environmental conditions across the landscape, whereas males respond to pressures to disperse. In insects, smaller females are usually associated with lower fecundity (Kozłowski, 1992; Honěk, 1993). Therefore, the demographic changes we see in the short term, of significant decline in the matrix (Evans *et al.*, 2017), might be expected.

New habitat selects for increased head width among females

We also found that females had increased interocular width compared with males by 2009–2013. A larger head width

can be related to the ability to consume larger food items (Pearson & Stemberger, 1980; Laparie *et al.*, 2010). Most carabids, including *N. resplendens*, are predators, and therefore prey availability is a key habitat determinant (Niemelä, 1993; Koivula *et al.*, 1999). Further, food is a vital resource needed for arthropod reproduction (Juliano, 1985; Sota, 1985). This could indicate that females, under pressure from a novel environment, i.e. the plantation, have adapted to different food resources to be able to invest in reproduction.

Phenotypic plasticity or gene frequency changes?

A question that follows the findings of this study is whether the morphological changes that we have documented result from phenotypic plasticity or changes in gene frequencies. Phenotypic plasticity is the ability of a genotype to produce different phenotypes in response to different environmental conditions (Fusco & Minelli, 2010; Pigliucci, 2010). In the case of beetles, phenotypic plasticity is known to play a large role in this group's response to environmental change (Fusco & Minelli, 2010; Gotoh *et al.*, 2014; Ozawa *et al.*, 2016). For example,

horned beetles (subfamilies Dynastinae and Scarabaeinae within the Scarabaeidae family) demonstrate marked morphological differences in horn shape and overall body size in response to differing food availability during larval development (Valena & Moczek, 2012). Further, these changes, as with *N. resplendens*, are sexually dimorphic and are usually only manifested in the males of these species. Smaller horned beetle males, instead of investing in horns for combat with other males over females, invest in non-aggressive tactics such as enlarged testes and ejaculate volumes to aid in sperm competition (Tomkins & Simmons, 2000). It is possible, therefore, that the morphological changes we see in *N. resplendens* in response to the landscape changes at Wog Wog are as a result of the phenotypic plasticity inherent in this species. The alternative is a change in the frequency of alleles relevant to morphology between the land cover types in the Wog Wog landscape. However, to determine this directly, genetic research is needed on this species at Wog Wog. Local adaptation to spatially varying environmental conditions can be swamped by migration (gene flow) when the scale of environmental heterogeneity is much finer than the scale of dispersal (Blanquart *et al.*, 2012; Forester *et al.*, 2016). Potentially, the scale of environmental heterogeneity may be too fine for strong local adaptation to fragmentation-related environmental conditions in our study landscape. This could be informed by studies of spatial patterns of genetic structure (allele frequency differentiation) and gene–environment analyses to identify signatures of environmental selection (Schoville *et al.*, 2012).

Morphological changes at the landscape scale

The strong relationship between effect sizes in the fragments and effect sizes in the matrix for all traits indicates that the selection pressures are acting across the whole landscape of the treatments. It could also mean that the populations are continuous between these habitats.

Morphological changes in response to environmental change

Morphological adaptation is gaining more attention as a mechanism behind how species respond to environmental change (Nicotra *et al.*, 2015). Despite being one of the longest-running experiments of its kind, the morphological changes we see at Wog Wog appear over relatively short time periods, during a time of constant change to the environment in which these species inhabit. The insights gained demonstrate that species are able to adapt in short timescales, but also add an extra dimension to understanding how species respond to environmental change. A species' adaptive capacity has the potential to change how it can cope with environmental change (Dawson *et al.*, 2011; Nicotra *et al.*, 2015). Therefore, considering this adaptive capacity is potentially very important for the management of species through future environmental change (Bell & Gonzalez, 2009; Desrochers, 2010; Nicotra *et al.*, 2015). Furthermore, we have demonstrated the importance of museum specimens, such as those collected during the history of Wog

Wog, as a resource for monitoring how species respond to landscape change (Desrochers, 2010) and offer great potential for insights into evolution of species in natural habitat over time (Holmes *et al.*, 2016), in turn providing information regarding their capacity to adapt to environmental change.

Conclusions

The landscape presented at the mature stage of the pine plantation selects for individuals of *N. resplendens* with increased dispersal ability, which is exhibited as an increase in overall size and leg length. Furthermore, the plantation seems to have driven divergence in dispersal ability between the sexes, probably as a result of the need for reproduction in females offsetting the selection pressures for increased traits related to movement. The pressures to change morphologically in the short term seem to have lasted over the long term, despite the population responses to fragmentation differing during this time. It might be possible, therefore, that early morphological change in the short term has helped to facilitate population increases in the matrix in the long term. Evidence that tests the dispersal strategies of this and other species using tracking studies (Ranius & Hedin, 2001; Hedin & Ranius, 2002; Ranius, 2006) or population genetics (Brouat *et al.*, 2003; Matern *et al.*, 2008) would improve our understanding of why these species respond to habitat change with differing population and morphological responses. Our results demonstrate that species can adapt to environmental change over very short time periods and underline the importance of considering adaptive capacity in the management of species in the face of future environmental change.

Acknowledgements

We thank the many people that have been involved in the establishment and maintenance of the Wog Wog Habitat Fragmentation Experiment, including Chris Margules, Mike Austin, and A. O. (Nick) Nicholls. We are grateful to all those who have helped with fieldwork over the history of the experiment, particularly George Milkovits. Thanks to the Forestry Corporation of New South Wales for their cooperation and assistance in the day-to-day running of the experiment. We would also like to acknowledge John Lawrence and Andy Hicks for their taxonomic work on the beetles in the Wog Wog collection. We thank Brett Melbourne for statistical advice and more generally for his help on this project. We also thank Janet Gardner for advice early on in the project. We thank the Australian National Insect Collection (ANIC), CSIRO, and its staff; especially Nicole Fisher, Cate Lemann and Beth Mantle. Funding to collect samples between 2009 and 2013 was provided by NSF DEB 0841892 to KFD. KFD was also supported by NSF DEB 1350872. MJE was funded by an Australian National University PhD Scholarship. The authors have no conflicts of interest to declare.

MJE led the conceptualisation with advice from SCB, PSB, KFD and DAD; MJE and KFD collected the data; MJE led the analysis with advice from SCB, PSB, KFD and DAD; MJE led the writing; and SCB, PSB, KFD and DAD made contributions to manuscript revisions.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12498

Table S1. Summary of individual carabids caught, and from which of the main treatments of year block and treatment of *Notonomus resplendens*.

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Accepted 27 November 2017

Associate Editor: Michael Bonsall