Title: Sexual selection predicts the persistence of populations within altered environments

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Abstract

The effect of sexual selection on species persistence is unclear. The cost of bearing ornaments or armaments might increase extinction risk, but sexual selection can also enhance the spread of

35 beneficial alleles and increase the removal of deleterious alleles, potentially reducing extinction risk. Here we investigate the effect of sexual selection on species persistence in a community of thirty-four species of dung beetles across a gradient of environmental disturbance ranging from old-growth forest to oil palm plantation. Horns are sexually selected traits used in contests between males, and we find that both horn presence and relative size are strongly positively associated with

40 species persistence and abundance in altered habitats. Testes mass, an indicator of post-copulatory selection, is, however, negatively linked with the abundance of species within the most disturbed habitats. This study represents the first evidence from a field system of a population-level benefit from pre-copulatory sexual selection.

Introduction

Sexual selection is ubiquitous across the animal kingdom, driving the evolution of traits which give advantages in competition for matings and fertilisations (Darwin 1871; Andersson 1994). Such traits are typically costly to produce and maintain, and are often honest indicators of an individual's condition, with their degree of expression reflecting underlying genetic quality via the 'genic capture' mechanism in many cases (Rowe & Houle 1996; Tomkins *et al.* 2004; Cotton & Pomiankowski 2007). By skewing individuals' reproductive success, sexual selection has the capacity to have profound effects on the fitness and viability of populations (Holland & Rice 1999; Lumley *et al.* 2015), particularly when a population faces stressful environmental change (Fricke & Arnqvist 2007; Long *et al.* 2012), but the picture is a complex one with both negative and positive effects of sexual selection potentially operating at the population level (Candolin & Heuschele 2008; Holman & Kokko 2013).

Of the potential negative effects, the straightforward costs to individuals arising from the effects of strong sexual selection are numerous. Sexual ornaments and weapons are costly to grow and to carry (Bobek *et al.* 1990; Rico-Guevara & Hurme 2018), sexual display and contests with rivals can be exceedingly expensive energetically (Hunt *et al.* 2004) and bring a risk of injury, and the increased conspicuousness of sexual display traits and need for movement to find potential mates can increase the risk of predation (Godin & McDonough 2003; Kuchta & Svensson 2014). Additionally, sexual selection reduces effective population sizes (Kokko & Brooks 2003) and may erode genetic variation Dugand *et al.* 2019, but see also Radwan *et al. 2016*). Models incorporating this additional selection load imposed by sexual selection find that the probability of extinction can be increased (Lande 1980; Tanaka 1996; Kokko & Brooks 2003) under certain circumstances (Martínez-Ruiz & Knell 2017).

Further to these costs of sexual selection, there are potential negative impacts at the population level arising from the effects of sexual conflict (Arnqvist & Rowe 2005): if traits which are beneficial to the fitness of one sex act antagonistically in the other sex, causing reduced fitness, then this can

70   reduce adaptation rates (Holland 2002; Rundle *et al.* 2006; Chenoweth *et al.* 2015), impede the

removal of deleterious alleles (Arbuthnott & Rundle 2012) and reduce the net reproductive rate of

the population (Holland & Rice 1999). A study of sex ratios and male harassment in common lizards

Lacerta vivipara, (Le Galliard *et al.* 2005) suggested that sexual conflict could even cause extinction

via a positive feedback loop whereby male harassment causes mortality of females, leading to a

75   male-biased sex ratio which then causes stronger selection for aggressive males, causing further

female mortality and ultimately driving the population to extinction. Modelling (Rankin *et al.* 2011)

suggests that this scenario is indeed plausible.

By contrast, a body of other research suggests that sexual selection could have beneficial effects at

the population level. Theory indicates that when there is strong reproductive skew sexual selection

80   can increase adaptation rates to novel environments: if the skew is in favour of 'high quality'

individuals this enhances the spread of adaptive alleles throughout a population (Lorch *et al.* 2003;

Martínez-Ruiz & Knell 2017). Consistent with this theory, laboratory studies using invertebrate

model organisms in experimental evolution designs have found that sexual selection enhances

adaptation and protects against extinction (Fricke & Arnqvist 2007; Long *et al.* 2012; Plesnar-Bielak

85   *et al.* 2012; Jacomb *et al.* 2016; Parrett & Knell 2018; Yun *et al.* 2018). Similarly, sexual selection has

also been found to enhance the removal of deleterious alleles and to reduce the probability of

extinction from inbreeding depression (Jarzebowska & Radwan 2010; Lumley *et al.* 2015). A recent

meta-analysis of 65 laboratory experimental evolution studies found that overall there is a

significant positive effect on traits associated with population fitness when sexual selection is strong,

90   especially when under environmental stress (Cally *et al.* 2019).

Taken as a whole, therefore, laboratory experiments suggest that at the population level the overall

effect of sexual selection is likely to be positive (Cally *et al.* 2019), although this will depend on the

specific system, the environmental conditions (Yun *et al.* 2018), and the nature of genetic variation

within a population (Dugand et al. 2019). Field studies, however, using comparative techniques and

95   largely focussed on vertebrates, suggest that sexual selection either increases extinction risk (McLain

et al. 1995; McLain & Vives 1998; Sorci *et al.* 1998; Doherty *et al.* 2003; Morrow & Pitcher 2003; Bro-

Jørgensen 2014; Martins *et al.* 2018) or has no effect on population level fitness (Prinzing *et al.* 2002;

Morrow & Fricke 2004). As an example, multiple studies have found that artificially introduced

populations of sexually dichromatic bird species are less likely to become established on islands

100   when compared to sexually monochromatic species (McLain *et al.* 1995, 1999; Sorci *et al.* 1998) but

see also (Donze *et al.* 2004; Moulton *et al.* 2009). Taking a different approach, Martins *et al.* (2018)

recently found that over geological timescales prehistoric ostracod species with a high intensity of

sexual selection, as predicted from sexual dimorphism in both size and shape, were more likely to

become extinct compared to species with relatively weak sexual selection.

105   There is, therefore, a mismatch between the findings of laboratory studies of invertebrate

populations, and field studies which tend to focus on communities of vertebrates, often with small

population sizes which could lead to an overriding effect of demographic stochasticity (Martínez-

Ruiz & Knell 2017). In order to attempt to resolve this, we examined the effect of sexual selection on

the persistence of tunneller dung beetle (Scarabaeidae: Scarabaeinae) populations after the

110   alteration and modification of tropical rainforest in Sabah, Malaysian Borneo. Beetles were sampled

across a replicated gradient of habitat disturbance ranging from old growth forest (OGF) through

selectively-logged (SLF) and heavily-logged forest (HLF) to oil palm plantation (OPP) (Ewers *et al.*

2011). Thirty-four species of tunneller dung beetle were found in the OGF, and the persistence and

abundance of each of these was followed across the gradient of environmental alteration; thus we

115   restricted the analysis to the tunneller species that were present in the undisturbed environment.

The intensity of sexual selection in each species was estimated using surrogates of pre-copulatory

sexual selection: whether a species is horned or hornless, and relative size of horns. Relative testes

mass was also recorded as a measure of post-copulatory sexual selection. Measures such as these

are used widely to estimate the intensity of sexual selection between species (Andersson 1994;

120   Hosken 1997; Byrne *et al.* 2002; Morrow & Pitcher 2003; Morrow & Fricke 2004; Bro-Jørgensen

2007, 2014; Simmons *et al.* 2007). We find that horn presence, and within horned species horn

length, both predict species persistence and abundance across the disturbance gradient, and we find

evidence linking higher testes mass to reduced abundances.

Methods

Study sites were located within the Stability of Altered Forest Ecosystems (SAFE) project site (4°33'N, 117°16'E) and the Maliau Basin Conservation Area (4°49'N, 116°54' E) in Sabah, Malaysian Borneo. The SAFE project is a large scale experiment investigating the effects of rainforest modification and fragmentation, consisting of a mixture of selectively logged and heavily logged lowland dipterocarp

130   rainforest, and oil palm plantations which were planted between 2000 and 2006 (Ewers *et al.* 2011). The SAFE project has been specifically designed to address the large-scale effects of forest fragmentation and disturbance in a well replicated design that controls for environmental variation (see Ewers *et al.* 2011 for further details). Sampling of dung beetles was carried out across a gradient of forest modification: old growth forest (OGF) in Maliau Basin, and within SAFE, in twice selectively

135   logged continuous forest (SLF), twice heavily logged forest (HLF), and oil palm plantation (OPP). The experimental fragmentation described by Ewers et al. (2011) had not yet taken place and so these 'fragments' are classified as heavily logged forest (HLF) within this study. For details in the differences in intensity of logging and forest cover between sites see Ewers *et al.* (2011) and for details of a number of abiotic factors see Hardwick *et al.* (2015). Dung beetle sampling was

140   performed between January and February in 2011 (Slade *et al.* 2019) to estimate abundance and species richness across the disturbance gradient, and to collect data on horn presence and relative lengths across the community. Between July and August in 2015 sampling was carried in the same sites to collect data on testes mass and increase sample sizes for relative horn lengths across the community.

145   In total, data from 108 traps from 2011 were used to determine species richness and abundance data across the landscape. Each habitat type (OGF, SLF, HLF, OPP) had three replicates, with nine sampling points (second order points in the sampling design explained in Ewers *et al.,* 2011) per replicate. Spatial scaling differed in HLF (Ewers *et al.* 2011) and nine second order points from three replicates (Fragments B, D and E in Ewers *et al.* 2011) were randomly selected. In 2015 the traps

150 were set at the same locations except only 3 traps were set per replicate in SLF due to logistical

reasons as beetles used for testes dissections needed to be live trapped and collected within 24

hours.

In both 2011 and 2015 sampling was carried out using pitfall traps baited with 25g of human dung

protected from rain with a cover. Human dung is widely used as standardised bait in tropical forests

155 (Marsh *et al.* 2013) and attracts a wide variety of dung beetle species (Davis *et al.* 2001; Larsen *et al.*

2006). Trapping methods differed slightly between years; in 2011 pitfall traps were half filled with a

solution of water, salt and detergent which kills beetles as they break the water surface tension and

cannot escape, and traps were left for 48hrs before being collected. In 2015, as we were collecting

beetles primarily for testes measurements, live pitfall trapping was used. A plastic funnel minimized

160 beetle escapes and traps were collected after 24hrs.

Specimens from 2011 were stored in 90% ethanol and identified to species level using Boucomont

(1914) and Balthasar (1963) and publications describing Bornean Scarabaeinae (e.g. Ochi 1996), and

the reference collections at the Oxford University Museum of Natural History (OUMNH). Species that

could not be identified were given morphospecies numbers. Specimens from 2015 were identified in

165 the field.

Our study set out to test the persistence of species after the modification of forest habitat. Until

relatively recently primary old growth forest would have dominated the majority of the landscape

investigated in this study. To test for population persistence after the modification of habitat in the

disturbed sites, we therefore only include species that were found in OGF in our analysis and track

170 their persistence and abundance across the disturbance gradient. Additionally, dung beetles can be

separated into ecological guilds based on their method of dung removal and nesting behaviour

(Slade *et al.* 2007). Sexual selection is believed to operate differently within these guilds and the

expression of horns is strongly associated with tunnelling, rather than ball-rolling behaviour (Emlen

& Philips 2006). Since the presence and size of horns was the main proxy for precopulatory sexual

175   selection used here only tunneller species were included in the analysis. In total 34 tunneller species

were included in the final dataset (supporting information Table S4). When available, average body

size, composite horn length, body mass, and testes mass were calculated for each species (see

supporting information for details). For a number of species we were unable to calculate

morphology data due to males not being trapped and these species were therefore excluded from

180   trait specific analysis.

Statistical analysis was carried out by fitting a series of models to species richness of horned and

hornless species across the disturbance gradient. A further series of models were fitted to the

abundance of species across the disturbance gradient with each sexually selected trait as an

explanatory variable (species being horned or hornless, relative horn length and relative testes

185   mass). From each series of models, model comparison was made by comparing corrected Akaike

information criteria (ΔAICc) and we report all with non-negligible support (ΔAICc<10; for further

details of statistical analysis see supporting information).

190   **Results**

Of the series of statistical models fitted to assess how the species richness of horned and hornless

species changed across the disturbance gradient, two had non-negligible support (ΔAICc<10;

supporting information Table S1). Both of these included the interaction term between habitat type

and whether species were horned or hornless, indicating that the effect of disturbance on the

195   number of species persisting depends on whether the species in question were horned or hornless

(Fig. 1). The majority of the horned species found in OGF persisted in SLF but the species richness of

hornless species declined markedly. Both horned and hornless species were substantially reduced in

HLF when compared to OGF. Strikingly, no hornless species were found to persist into OPP, whereas

11 of the 22 horned species found in OGF persisted across the disturbance gradient into OPP.

200   A similar pattern emerged when the abundance of horned and hornless species was analysed across

the disturbance gradient. Once again, two of the models which were fitted had non-negligible

support (ΔAICc<10), and both included the interaction term between habitat type and whether a

species was horned or hornless (supporting information Table S2). The interaction term appears to

be largely driven by hornless species having reduced abundance in SLF, in contrast to horned species

205   which tend to maintain similar abundance to OGF (Fig. 1). A similar but weaker pattern is also

observed within HLF in which the abundances of both horned and hornless species are reduced. In

OPP, hornless species are no longer found, and although the abundance of many horned species is

reduced compared to OGF, a number of them maintain high abundances. Qualitatively similar

patterns in species abundance were observed when taking phylogenetic relatedness into account by

210   fitting phylogenetic generalised linear mixed effects models (PGLMM; see supporting information for

details of molecular phylogeny). The model with the lowest AIC score included the interaction term

between habitat type and whether species were horned or hornless, however AIC differed by only

3.4 between the models fitted with and without the interaction (supporting information Table S3),

indicating that a component of the effect of horn presence could be attributed to closer

215   phylogenetic relationships between some species. Nonetheless, there is strong support overall for

the result that horned species tend to maintain higher abundances after the alteration of OGF

compared to hornless species.

As is typical for dung beetles (Emlen *et al.* 2005), there is considerable variation between horned

species in the degree of investment in horns, and this variability in relative horn size is likely to be

220   associated with differences in the intensity of male-male competition between species (Simmons &

Tomkins 1996; Bro-Jørgensen 2007). We therefore assessed the relationship between relative horn

size and abundance of horned species. Three models had non-negligible support (ΔAICc<10) and all

of these included the interaction term between relative horn size and habitat type (supporting

information Table S2). Overall, these models show an association between species abundance and

225   habitat disturbance, with reduced abundance within increasingly disturbed habitats. Species with

relatively large horns, however, tended to either maintain or have increased abundances compared

to baseline abundances (OGF) across the disturbance gradient, whereas those species with relatively

low investment in horns tended to show reduced abundance, with this effect being greatest within

the most disturbed sites (HLF and OPP; Fig. 2). PGLMMs showed a similar positive association

230   between relative investment in horns and abundance after habitat disturbance; in this case the

difference between AIC scores between models fitted with and without the interaction term

between habitat type and relative investment in horns was >10 (supporting information Table S3).

The model coefficients indicate that species with relatively large horns maintain similar abundances

to OGF within SLF and HLF, compared to species with relatively little investment in horns which tend

235   to have reduced abundances after the habitat is modified. Overall, there is strong support for an

effect of relative horn length influencing species abundance across the disturbance gradient.

Moreover, those species with relatively large horns tend to persist at high abundances compared to

those with little investment in horns.

Sexual selection can also occur post-copulation and relative testes size is known to correlate strongly

240   with the intensity of sperm competition a species experiences (Hosken 1997; Byrne *et al.* 2002; Simmons *et al.* 2007). We used relative testes mass as an estimate of the intensity of post-copulatory sexual selection. From the series of models fitted six had non-negligible support (ΔAICc<10), and of these the three with the lowest ΔAICc scores included the interaction term between testes mass and habitat type (supporting information Table S2). These models suggest that

245   species with relatively large testes have reduced abundance in HLF and OPP compared to species with relatively small testes, with no effect of testes mass on species abundance in OGF and SLF, although this effect is hard to visualise (Fig. 3). The remaining three models with non-negligible support, however, do not show this same relationship: one retains the main effects of habitat and testes mass and the remaining two just the main effect of habitat, indicating that the degree of

250   support for an effect of relative testes mass on species abundance across the disturbance gradient is less than the support for effects of horn presence and relative horn length (see above). The PGLMM containing the interaction term between relative testes mass and habitat type was the best fitting and the difference in AIC scores was 4.9 between the models with and without the interaction term included (supporting information Table S3). The model estimates indicate similar effects as non-

255   phylogenetic models: species with relatively large testes have reduced abundance in HLF and OPP compared to their abundances in SLF, however, in the least disturbed habitats (OGF & SLF) there was no effect of testes mass on species abundance. Together these results indicate some support for a negative effect of relative testes mass on species persistence within the most disturbed habitats.

260   **Discussion**

As the intensity of disturbance increases species associated with old growth forest (OGF) are progressively lost, with those remaining tending to have reduced abundances. Such patterns have been observed in dung beetle communities before (Slade *et al.* 2011; Braga *et al.* 2013; Gray *et al.* 2014; França *et al.* 2017) and are likely to be a common pattern across a wide variety of taxa (Sodhi

265   *et al.* 2004; Gardner *et al.* 2009; Bicknell *et al.* 2014; Thorn *et al.* 2018). Here we find evidence that this loss of species with disturbance is reduced in horned species. Furthermore, within the horned species there is an effect of relative horn size, whereby a high degree of investment in horns is associated with larger population sizes and improved persistence after habitat modification. We also find a negative relationship between relative testes mass and abundance, although only in the two

270   most disturbed habitats.

Our findings that species possessing horns and, if horned, those species with relatively large horns have increased persistence across the disturbance gradient are largely consistent with theoretical predictions (Lorch *et al.* 2003; Martínez-Ruiz & Knell 2017) and the majority of laboratory studies (Cally *et al.* 2019) which suggest that sexual selection acts to purge populations of deleterious alleles

275   and drive adaptive evolution. On the basis of this theory, we can propose a mechanism for this pattern. Expression and exaggeration of horns is known to be condition dependent in dung beetles (Emlen 1994; Knell & Simmons 2010), and so those males with the largest horns are likely, on average, to be better adapted to the environment or to be carrying a lower mutational load than others. In those species that express horns, intrasexual competition is likely to be more intense

280   compared to hornless species, and in those species with a relatively high investment in horns it is likely to be more intense compared to those with a relatively low investment in horns. This increased intensity of competition is likely to lead to well-adapted males or those with low mutational loads, as signalled by their large horns, being able to monopolise mating opportunities (Hunt & Simmons 2001; Karino *et al.* 2005; Pomfret & Knell 2006). Sexual selection therefore could be skewing

285 reproductive success in favour of 'high quality' individuals, providing population-level benefits of

competition between males and increasing the likelihood that species under strong pre-copulatory

sexual selection are more likely to persist after environmental change.

The population-level benefits of male-male competition found here contrast with the finding that

relative horn length in bovids is positively associated with extinction risk (Bro-Jørgensen 2014), and

290 these data are also apparently at odds with a number of previous field studies, which found sexual

selection to increase the probability of extinction in novel environments (McLain *et al.* 1995, 1999;

Sorci *et al.* 1998). A number of possible explanations exist for this discrepancy. For example, before

habitat alteration, the populations in the current study would probably have been at or near their

natural carrying capacities, whereas many previous studies focussed on the persistence of small or

295 very small populations of introduced birds (McLain *et al.* 1995, 1999; Sorci *et al.* 1998). It has been

suggested that strong sexual selection could make small populations such as the ones addressed in

these studies of birds particularly prone to extinction due to increased demographic stochasticity,

whereas large populations would benefit from strong sexual selection (Martínez-Ruiz & Knell 2017),

which is consistent with the current study. Furthermore, generation time can influence the adaptive

300 capacity of populations (Chevin *et al.* 2010). Although little is known about generation times for the

animals studied here, dung beetles typically have short development times (Simmons & Kotiaho

2002), and therefore increased potential to adapt compared to those previous studies on species

with relatively long generation times such as birds and mammals (McLain *et al.* 1995, 1999; Sorci *et

al.* 1998; Doherty *et al.* 2003) — it is possible that this increased adaptive capacity could interact

305 with the strength of sexual selection to enhance population persistence.

The patterns we describe could, alternatively, arise if horned species are able to outcompete

hornless species, and if species with relatively large horns outcompete those with relatively small

horns for resources within habitats which are structurally less complex (i.e. disturbed habitats).

Indeed, within the mite, *Rhizoglyphus echinopus*, aggressive male morphs have been shown to

310   outcompete benign male morphs in less complex habitats (Tomkins et al 2011). Although we cannot

explicitly reject this idea it seems unlikely in this case for several reasons. Firstly, in dung beetles the

majority of interspecific resource competition will occur between females, which rarely express

horns. Secondly we are unaware of any literature indicating that horns (male or female) in dung

beetles are used in interspecific competition, and thirdly, although the ecological complexity is,

315   overall, greater in the least disturbed sites, the actual space in which resource competition will be

occurring (i.e. a dung pile or tunnel) is likely to remain similar between habitats.

In contrast to the positive effects of pre-copulatory sexual selection, we found a negative effect of

relative testes mass on species abundance within the most disturbed habitat types. Like horns,

testes mass can be condition-dependent in dung beetles (Knell & Simmons 2010; Almbro & Simmons

320   2014) and this is likely to be the case within the species studied here. Male animals are known to

trade-off investment in traits associated with pre-copulatory success against traits associated with

post-copulatory success (Simmons *et al.* 2017), so this pattern could potentially arise if horn size

and/or presence is negatively correlated with testes mass. In other tunnelling dung beetles the

evolution of longer horns has been found not to be associated with reductions in testes mass

325   (Simmons & Fitzpatrick 2016). Additionally, in our dataset mean testes mass did not differ between

horned and hornless species, and within the horned species there is no evidence for a relationship

between horn length and testes mass (see supporting information). This indicates that the observed

negative relationship between testes mass and abundance is not likely to simply be an artefact of

the relationship between investment in horns and testes.

330   This negative relationship is, however, consistent with the findings that increased sperm competition

and polyandry, predicted from testes size in birds (Morrow & Pitcher 2003) and sexual dimorphism

in ostracods (Martins *et al.* 2018), are positively associated with extinction risk and extinction,

respectively. In line with previous work, this finding highlights the possibility of trait-specific costs

and benefits (Morrow & Pitcher 2003; Bro-Jørgensen 2014). For example, if horned, dung beetle

335　species with larger testes are predicted to have increased proportions of 'minor' males adopting alternative mating strategies (Simmons *et al.* 2007), this is likely to reduce reproductive skew in male populations and possibly negate the beneficial effects of pre-copulatory sexual selection in this system. It is also possible that the increased level of polyandry associated with larger testes may decrease levels of paternal provisioning (Ball *et al.* 2017) and reduce the reproductive potential of

340　stressed populations further.

The negative relationship between testes mass and abundance could also arise if increased mating rates and levels of sperm competition reduce female fitness via harmful male traits such as seminal fluids (Chapman 2001) or mechanical damage (Arnqvist *et al.* 2005) and therefore reduce overall population fitness (Holland & Rice 1999). Although we do not know the strength of sexual conflict in

345　the species studied here it seems an unlikely explanation for this observation because in *Onthophagus taurus*, a congeneric of many of the species in the current study, there is little evidence of strong sexual conflict, with multiple female matings leading to higher female fitness (Simmons & García-González 2008; Garcia-Gonzalez & Simmons 2011; Simmons & Holley 2011).

This is the first study of wild populations to find a positive effect of pre-copulatory sexual selection

350　at the population-level and find evidence indicating that species with increased intensity of male-male competition are more likely to persist after modification of the environment. Understanding which species may be particularly prone to extinction after environmental change is important when evaluating species conservation status and management practices. Due to sexual selection being ubiquitous in sexually reproducing species, further knowledge of its influence on population fitness

355　within our rapidly changing world is becoming increasingly important.

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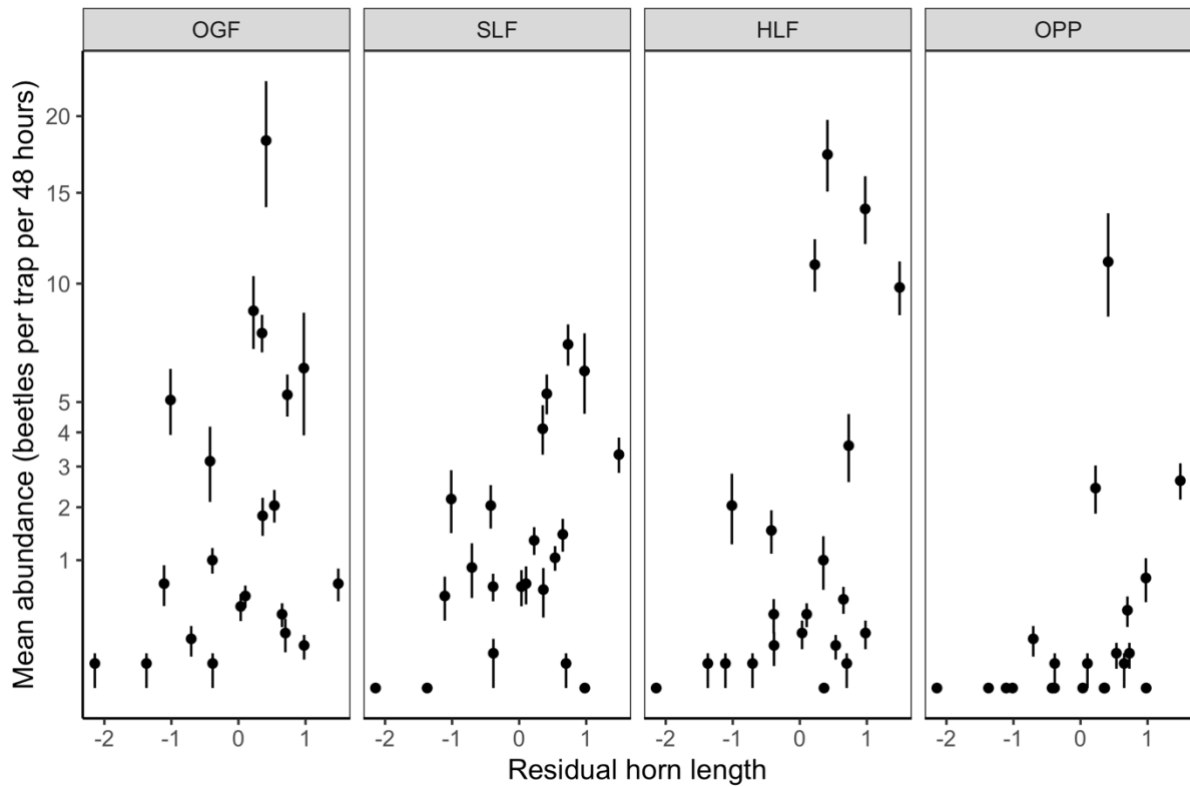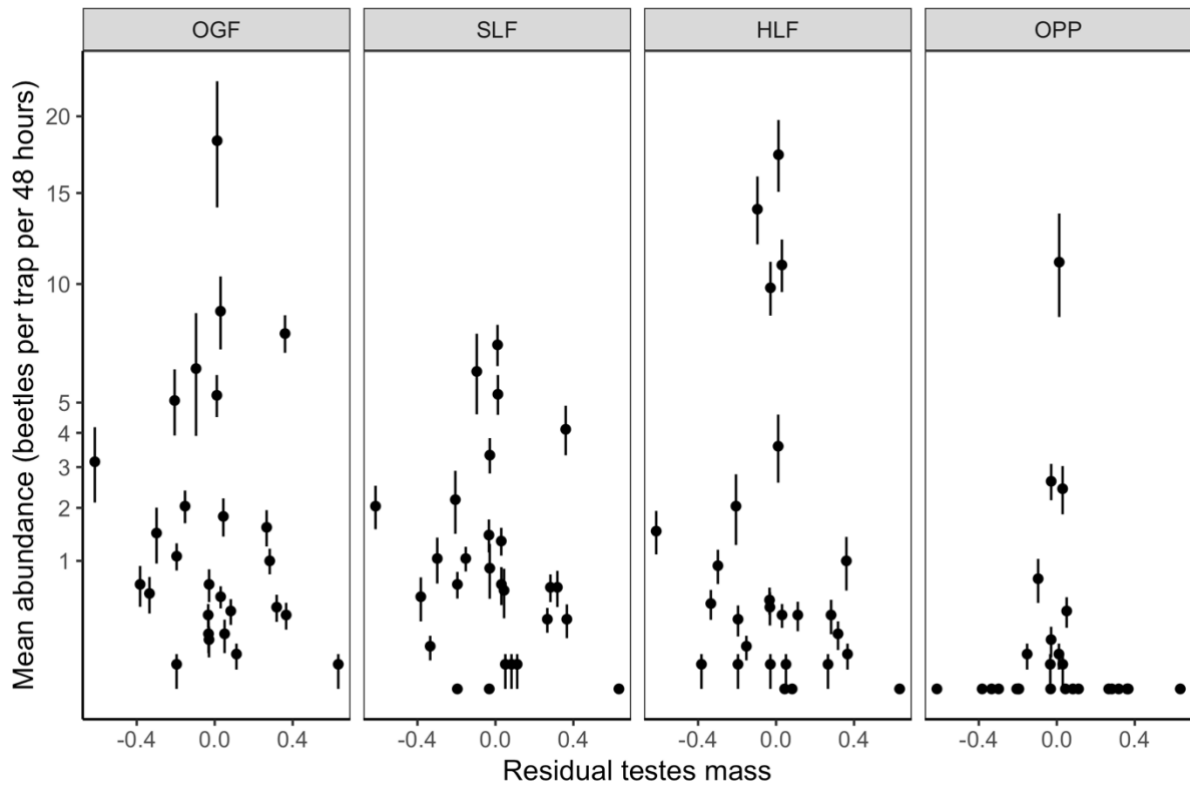
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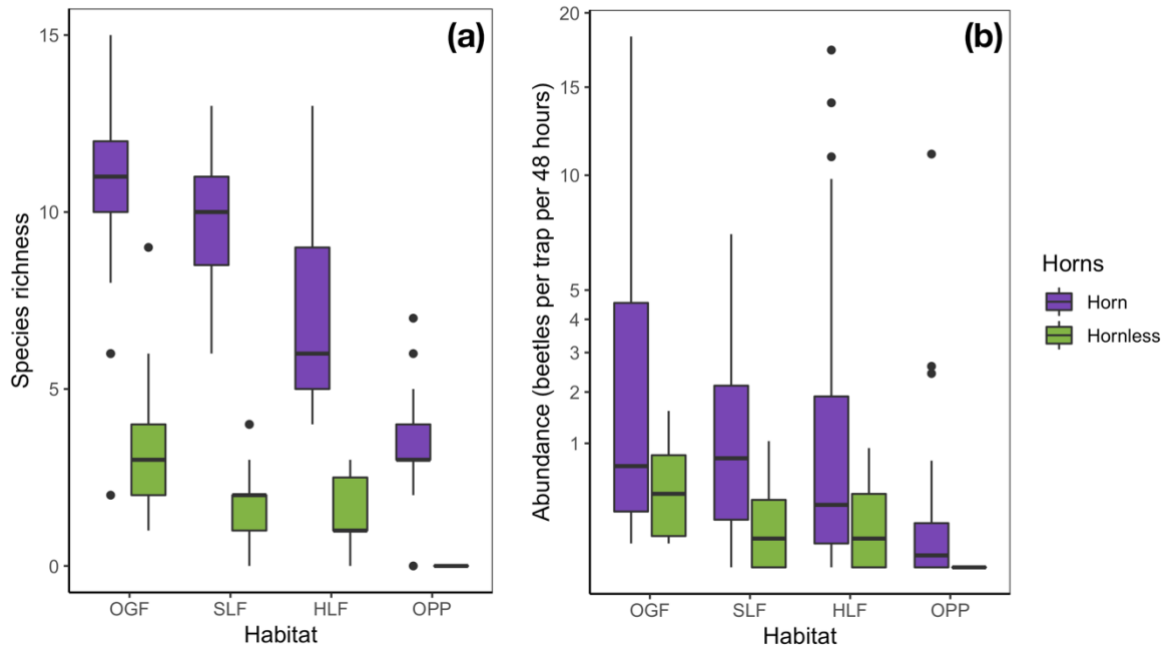
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Figure 1: The effect of species being horned or hornless on (a) species richness and (b) abundance of species in each trap across the disturbance gradient: old growth forest (OGF), selectively logged forest (SLF), heavily logged forest (HLF), and oil palm plantation (OPP). The y-axis in *b* is on a square-root scale to improve visualisation of data.

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Figure 2: The effect of investment in horns after controlling for the effect of body size (residual horn size from a log-log transformed regression of horn length on body size, used here for illustrative purposes) on the mean abundance of species per trap across the disturbance gradient: old growth forest (OGF), selectively logged forest (SLF), heavily logged forest (HLF), and oil palm plantation (OPP). The y-axis is on a square-root scale to improve visualisation of data and error bars indicate SE.

585 **Figure 3:** The effect of testes mass after controlling for effect of body mass on the mean abundance of species per trap across the disturbance gradient: old growth forest (OGF), selectively logged forest (SLF), heavily logged forest (HLF), and oil palm plantation (OPP). The y-axis is on a square-root scale to improve visualisation of data and error bars indicate SE. As for fig. 2, residual testes mass from a log-log regression of testes mass on total body mass is used to represent relative testes mass for illustrative purposes only.

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