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Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition

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Running title: Insects and carrion decomposition

Abstract

1. Ecological processes are maintained in different environments by different species performing similar functional roles. Yet, little is known about the role of the environment in shaping insect biodiversity associated with a process that is ephemeral and patchy.

2. We quantified experimentally the mass loss of carrion in response to contrasting habitat types (grassland or tree), and the presence, diversity, and composition of insect assemblages. We also examined differences in insect assemblages between these two habitats.

3. We found that the presence of insects led to a doubling in mass loss, but that grassland or tree habitat type had no effect on this process. By contrast, habitat type had a significant effect on the composition of generalist ant and beetle assemblages, but not on specialist fly assemblages. Given the colonisation of insects, carrion mass loss was negatively associated with increasing evenness of fly assemblages and increasing ant abundance. We also found that variation in fly assemblage composition was correlated with variation in carrion mass loss.

4. Our study highlights the major role of habitat type in shaping the composition of generalist insects at carrion, but the minor role in affecting specialist and highly vagile insects. This complements our findings that insect colonisation of carrion was critical to accelerated mass loss, and that fly assemblages were responsible for variation in this process, regardless of habitat. Our study sheds new light on the contribution of insect biodiversity to decomposition in variable environments, with consequences for carrion food webs and nutrient cycling.

Keywords: ants, beetles, flies, biodiversity, carcass, carrion, decomposition, saprophage

Introduction

The role of biodiversity in maintaining ecological processes is a topic of immense interest (Reiss et al., 2009), and is particularly relevant to landscapes undergoing anthropogenic change and biodiversity loss (Hooper et al., 2012). This is because the loss of particular species can result in changes to key ecological processes, with potential ramifications for broader functioning of an ecosystem. Identifying which species are involved in different ecological processes, and the consequences of changes to their abundance, diversity or composition on ecological process rates is therefore fundamental to the understanding of ecosystems.

The decomposition of dead organic matter is a key ecological process central to the ecosystem function (Swift et al., 1979), and is performed by a diverse array of microbial and invertebrate species (Gessner et al., 2010; Moore et al., 2004). Compared with the widespread and predictable occurrence of dead plant matter, however, dead animals (i.e. carrion) are an unpredictable, patchy, and ephemeral resource (Barton et al., 2013a; Finn, 2001). These distinctive spatial and temporal properties of carrion, and the far greater emphasis on the study of plant-derived biomass (Benbow et al., 2015a; Handa et al., 2014), means less is known about the ecological drivers of variability in carrion decomposition, and the role of the environment in shaping insect communities involved with this process (Benbow et al., 2015b; Doube, 1987; Farwig et al., 2014).

There is a rich literature documenting both the vertebrate (Beasley et al., 2015; DeVault et al., 2003; Moreno-Opo & Margalida, 2013) and insect (Fuller, 1934; Merritt & De Jong, 2015; Payne, 1965; Putman, 1978) biota found at carcasses. In the absence of vertebrate scavengers, for example, it is well established that key families of flies (e.g. Muscidae, Calliphoridae) have an important role in the consumption of carrion (Payne, 1965). Yet much of this knowledge has been generated from the forensic, livestock or disease science disciplines (Fuller, 1934; Merritt & De Jong, 2015; Payne, 1965). By contrast, the ecological study of insect carrion fauna has stemmed from questions related to meta-population theory (Hanski & Gilpin, 1991), species coexistence (Hanski, 1987; Ives, 1991; Kouki & Hanski, 1995), and resource partitioning among the various specialist and generalist components of species assemblages (Braack, 1987; Merritt & De Jong, 2015). As a result, there are very few studies that have examined the role of insect assemblages in the carrion decomposition process, including the effects of different taxa, or their diversity and composition, on decomposition rate (Farwig et al., 2014; Pechal et al., 2014).

The broad aim for our study was to determine how variation in the environment affects the ecological process of carrion decomposition and its associated insect community. We conceptualized our aim as a set of inter-related factors involving insects, habitat and carrion, which we then used to develop specific questions to examine how insects and the environment affected carrion mass loss. Our questions were:

(i) *How does habitat type or the exclusion of insects affect carrion mass loss?* Previous studies have indicated to varying degrees that carrion decomposition rate is affected by the exclusion of insects (Pechal et al., 2014) and surrounding habitat (Farwig et al., 2014) . Yet these particular studies did not take a quantitative approach to measuring decomposition rate, focused on only particular components of the carrion insect community, or evaluated environmental gradients over large scales. Our study tested the effect of the exclusion of insects and contrasting habitat type on a quantitative measure of carrion decomposition. We predicted that both factors would affect mass loss, but were uncertain of their relative importance due to the unknown role of habitat type in shaping the carrion insect community in our study landscape.

(ii) *Does habitat type affect the diversity or composition of insect assemblages at carrion?* Differences in habitat are known to drive variation in insect assemblages (Barton et al., 2009; Lessard et al., 2011). Less is known about the role of habitat in driving variation in insect assemblages associated with carrion, where the carrion itself may be viewed as habitat. We therefore examined the responses of insects at carrion collected from two distinct habitat types, and considered insects from both a taxon-specific (flies, beetles, ants) and functional group (saprophages, predators) perspective. This is because many carrion-associated insects have evolved dispersal and behavioural traits that enable the rapid location and colonisation of patchy and unpredictable resources such as carrion (Barton et al., 2013b; Tomberlin et al., 2011). We predicted, therefore, that vagile flies and saprophages would display a weaker response to habitat type than generalist predators and ground-active beetle or ant taxa.

(iii) *Does the diversity or composition of insect assemblages affect carrion mass loss?* Given insect colonisation of carrion (i.e. continuing from Q1), we wanted to know if the diversity of composition of different components of the carrion insect community affected decomposition rate. Unlike for plant litter (Handa et al., 2014; Jonsson & Malmqvist, 2000), few studies have explicitly examined the effect of insect diversity or composition on carrion mass loss (Farwig et al., 2014). We predicted that flies or saprophages would be most likely to have an effect on carrion mass loss due to their direct role in carrion consumption, and the presumed limited potential for predators, beetles, or ants to dramatically alter the decomposition rate.

Our study allows us to make conclusions about the functional role of different components of the carrion insect community, and the interplay between resource specialization and environmental filtering of insect assemblages. We discuss how carrion decomposition is robust to landscape variation due to the differential sensitivity of carrion specialists and generalists to habitat, which has implications for carrion food webs and nutrient cycling.

Materials and Methods

Study area and experimental design

We conducted our experiment in the Mulligans Flat – Goorooyarroo Woodland Experiment, an area of temperate eucalypt woodland reserve located 15km from the city of Canberra, southeastern Australia (35.165°S 149.171°E) (Shorthouse et al., 2012). The study area is characterized by areas of open grassland dominated by native perennials (*Themeda*, *Aristida*, *Rytidosperma*) and interspersed with stands of yellow box (*Eucalyptus melliodora*), red gum (*E. blakelyi*) and red stringy bark (*E. macrorhyncha*) trees (Barton et al., 2016; McIntyre et al., 2010). We selected 18 sites to place our carcasses – nine in open grassland and nine under trees (Fig. S1). Tree sites were defined by having an obvious canopy with continuous leaf litter on the ground, and were typically part of a stand containing several trees. Open grassland sites were defined by having continuous grass layer dominated by native perennial species, and were typically more than 80 m from the nearest tree. We paired each grassland site with the nearest tree site to form nine 'blocks' that aided in controlling for spatial variation among sites. The sites furthest from each other were separated by approximately 6000 metres (Fig. S1).

Carcasses, covariates and insect exclusion treatment

We deployed a rabbit carcass (*Oryctolagus cuniculus*) at each site (n=18). Rabbits were obtained from routine pest shooting operations conducted by the Australian Capital Territory (ACT) government. Only intact carcasses were used (average mass = 1750 g), and they were stored frozen until needed. Each carcass was placed in a random position and in direct contact with the ground inside a small cage-like structure (Fig. S2) to prevent scavenging by vertebrates such as foxes and ravens. Each structure also had a roof made from a white plastic sheet that provided shade through the middle of the day, thus reducing the effect of direct sunlight that differed between the open and tree environments.

Temperature is an important determinant of decomposition rate due to its strong regulation of insect, microbial, and biochemical activity (Conant et al., 2011; Swift et al., 1979). To account for variation in temperature among our sites, we recorded hourly temperatures using temperature data loggers (type DS1921G, Maxim Integrated Products) at each site over the duration of the experiment. We summed the hourly temperatures recorded over the 12-day period of the study (11 -22 January, 2016), and then divided by 24 to derive an accumulated-degree-day (ADD) value for each carcass. These data were fitted as a covariate in all analyses involving mass loss.

Eight sites (four grassland-tree ‘blocks’) had additional carcasses added in separate structures to form the insect exclusion treatment. Each of the eight carcasses were loosely wrapped in nylon insect-screen mesh (approximately 1mm diameter aperture), and were treated with a pyrethrum-based insecticide to prevent colonisation by insects. The experiment was allowed to progress until the onset of dry decay (day 12) in the rabbit carcasses with full insect access.

We then collected all carcasses and weighed them to the nearest gram. All loose plant matter, insect casings, and soil were removed prior to weighing, and loose fur or skin was retained. We calculated mass loss of each carcass by subtracting the final mass (g) from the starting mass (g).

Insect sampling and assemblage variables

We sampled insects using a single pitfall trap at each carcass. Each pitfall trap was positioned adjacent to the ventral surface of the rabbit carcass and away from any nearby structural habitat features such as logs or shrubs. Pitfall traps were approximately 250ml in volume (8cm diameter), and were half-filled with a glycol and ethanol solution. Traps and their contents were taken (and replaced) on days 1, 2, 3, 4, 6, 8, 10, and 12 following the deployment of the carcasses. We removed all adult ants, beetles, and flies from every sample, then counted and assigned each individual to a species or 'morphospecies' (sensu Oliver & Beattie, 1996), with all hereafter referred to as species. Identification was conducted using appropriate keys (Andersen, 1991; CSIRO, 1991; Kavazos et al., 2011; Matthews, 1982, 1984; Shattuck, 1999; Wallman, 2001). A reference collection was established, and species and morphospecies were verified as being distinct types with the assistance of taxonomists at the Australian Museum and the Australian National Insect Collection.

Flies, beetles and ants are the most numerous insect taxa found at carcasses in our study area (Barton et al., 2013b), and were each analysed as distinct taxa. However, we were also interested in the functional role of the insects at carcasses, and so assigned species to saprophage and predator trophic groups. These functional groupings were based on the literature (Barton et al., 2013b; Fuller, 1934; Shattuck, 1999; Wallman, 2001), with species assignments given in Table S1. Briefly, saprophages included all fly species and some beetle species, whereas predators included some beetle species and some ant species (Fig. S3). There is some overlap among the functional role of species, but we assigned species based on their dominant trophic role. For example, the fly *Chrysomya rufifacies* is known to prey on other fly larvae (Brundage et al., 2014) but here was considered primarily as a carrion feeder. Similarly, some ants will likely scavenge on carcass remains as well as prey on other insects (Shattuck, 1999), but this was not always clear. For this reason, we assigned only species of *Iridomyrmex* to the predator group based on field observations, and the numerical dominance (and thus potential functional significance) of this genus.

Statistical analysis

Question 1 - *Does habitat type or insect exclusion affect carrion mass loss?* To answer this question we used the full set of carcasses across our 18 sites (18 with insect access, 8 with insect exclusion, n=26). We used analysis of variance to test for effects of habitat type (grassland, tree), insect treatment (access, exclusion), and their interaction, on carcass mass loss (g). We also included accumulated-degree-days (ADD) as a covariate to account for potential temperature-dependence in mass loss, and fitted site as a blocking factor to account for spatial variation.

Question 2 - *Does habitat type affect the diversity or composition of insect assemblages at carrion?* For this question, we pooled insect samples to give one sample per rabbit carcass, which represented the aggregate insect community present during the entire decomposition period. Prior to statistical examination of insect assemblages, we removed all singleton species from our insect datasets as these were often incidental or transient species, and of little value in understanding broader community patterns. We were also interested in quantifying the thoroughness of our sampling, and so used the software EstimateS 9.1 (Colwell, 2013) to calculate species accumulation curves based on observed species richness and estimated 'true' richness (ACE and Chao 1) using 1000 randomisations of the data. We tested for an effect of habitat type on the abundance, species richness, evenness, and composition of five different components of the insect community: (i) flies, (ii) beetles, (iii) ants, (iv) predators, and (v) saprophages. First, we used generalized linear mixed models (Genstat 17, VSN International Ltd., 2016) to test for an effect of habitat type on the abundance or species richness of the five insect groups. We fitted site blocks as a random factor, and used a Poisson error distribution with a logarithmic link function. For evenness, we used linear mixed models with the same random effect and normal distribution. To examine compositional patterns, we used permutation-based multivariate analysis of variance (Permanova, Anderson, 2001) to test for an effect of habitat type on assemblage composition for the five insect groups. We applied a randomized block design that treated site as the blocking factor, and habitat as a fixed factor (McCune & Mefford, 2011). We then used Principle Coordinates Analysis (PCoA) to visually examine and interpret differences in assemblage composition between habitats. For multivariate analyses we used the Bray-Curtis dissimilarity metric on square-root transformed count data (McCune & Mefford, 2011).

Question 3 - *Does the diversity or composition of insect assemblages affect carrion mass loss?* To answer this question we used insect assemblage data from carcasses with full insect colonisation (n=18). First, we used Akaike Information Criterion (AICc) model selection in a linear modelling framework to identify the best insect predictors of carcass mass loss. For this analysis we used the 'lme4' (Bates et al., 2016) and 'MuMIn' (Barton, 2016) packages in R (R Core Team, 2016). Our explanatory variables included abundance, species richness, and evenness of flies, beetles, ants, predators, saprophages. Due to the non-independence of the taxon and functional group explanatory variables, we ran two models: one model including flies, beetles, and ants, and a second including predators and saprophages. The explanatory variables were on different scales, we therefore rescaled them all to between 0 and 1 using the 'scales' package (Wickham, 2016) in R. We fitted all possible subsets of our explanatory variables without interactions, and considered all competing models within two AICc units of the lowest AICc score (Burnham & Anderson, 2002). Second, we examined the effect of assemblage composition on carcass mass loss using Mantel tests. This allowed us to look for a significant correlation between pair-wise Bray-Curtis dissimilarity in insect assemblages and pair-wise Euclidean distance in mass loss among all carcass combinations. We performed separate Mantel tests for each insect group, used 999 permutations to calculate significance, and plotted the linear relationship for significant correlations.

RESULTS

Question 1. Does habitat type or insect exclusion affect carrion mass loss?

We found a highly significant effect of insect exclusion ($F_1 = 43.21$, $P < 0.001$) on carcass mass loss, but not habitat type ($F_1 = 0.48$, $P = 0.499$) or their interaction ($F_1 = 0.02$, $P = 0.903$). We also found no effect of the accumulated degree days covariate ($F_1 = 0.00$, $P = 0.985$). Mean mass loss of carcasses with full insect colonisation was twice that of carcasses with insect exclusion after 12 days (Fig. 1).

Question 2. Does habitat type affect the diversity or composition of insect assemblages at carrion?

We sampled 18,367 insects from 83 species, including 15 species of flies, 34 species of beetles, and 34 species of ants (Table S1). Species accumulation curves indicated very thorough sampling of the insect community, with observed species richness similar to estimated 'true' species richness for flies, beetles and ants (Fig. S4). We found a significant effect of habitat type on beetle and predator species richness, with more species found under trees than in grassland (Fig. 2), but no effect of habitat on any other assemblage measure for all five insect groups (Table 1). By contrast, permanova revealed significant differences in the composition of ant (F=14.45, P = 0.011), beetle (F = 3.822, P = 0.009), and predator (F=12.19, P = 0.005) assemblages between grassland and tree habitats. However, we found a small difference between saprophage assemblages (F=1.84, P = 0.028), and no difference in fly assemblages (F = 0.65, P = 0.742). Ordination plots showed no separation of fly assemblages based on habitat (Fig. 3a), and a weak separation of the broader saprophagous functional group (Fig. 3b). In line with the permanova tests, ordinations also showed strong separation of beetles (Fig. 3c) and ants (Fig. 3d), as well as the composite predator functional group (Fig. 3e).

Question 3. Does the diversity or composition of insect assemblages affect carrion mass loss?

Fly evenness and ant abundance were the variables that best predicted carrion mass loss when taking a taxonomic approach (Table 2a). Indeed, fly evenness was in all of the highest ranked competing models, indicating its overall importance. By contrast, no insect functional group predictors were better than the null model of carrion mass loss, indicating that no measure of insect functional groups had a particularly strong effect on carrion mass loss (Table 2b). Competing models, however, did include saprophage abundance or richness, or predator abundance, but had a higher AIC and lower r^2 than the taxon focused model with fly and ant predictors. The linear relationship between carrion mass loss and fly evenness (Fig. 4a) and ant abundance (Fig. 4b) show a negative association. Looking at fly assemblages more closely indicated rabbit carcasses with low evenness were dominated by the blowflies *Chrysomya varipes* and *Ch. rufifacies* (Fig. S5).

Effects of insect composition on carrion mass loss were confined to fly assemblages. Mantel tests revealed a significant correlation between pair-wise assemblage dissimilarity and carcass mass loss for flies ($r = 0.329$, $p = 0.024$), but not for beetles ($r = -0.011$, $p = 0.950$), or ants ($r = -0.016$, $p = 0.846$). Functional group responses showed no correlation for predators ($r = 0.010$, $p = 0.893$), and a weak correlation for saprophages ($r = 0.280$, $p = 0.059$). The linear relationship between pair-wise fly assemblage dissimilarity and carcass mass loss showed that greater difference in fly assemblages was associated with greater difference in carcass mass loss (Fig. 5).

DISCUSSION

We have shown the dominant role of insects and the comparatively minor role of habitat type in the decomposition of carrion in our study landscape. Further, we have revealed the large effect of habitat type on the beetle, ant, and predator components of the insect community, but smaller effect of habitat on saprophages and no effect on flies. This provides some compelling insight into how the process of carrion decomposition is maintained in variable environments, with the functional role of specialist carrion feeders (i.e. flies) apparently unaffected by the contrasting habitats. Below we discuss the main findings from our questions, the interplay between resource specialization and environmental filtering of insect assemblages, and their role in carrion decomposition.

Insect colonisation had a greater effect on decomposition than habitat

We found that only insect exclusion had an effect on carcass mass loss, with no effect of habitat type. The exclusion of insects from rabbit carcasses had a substantial slowing effect on decomposition rate, with only half the mass loss compared with carcasses that were allowed full insect access. This reflects other work that has demonstrated the importance of delayed insect access (Pechal et al., 2014), as well as complete insect exclusion (Payne, 1965). For example, the work by Payne (1965) showed that insects contributed to the decomposition of a juvenile pig carcass leading to approximately 90% mass loss after only five days, compared with only 30% mass loss in carcasses where insects were excluded. Our result was less extreme than this, which was probably due to differences in the animal model used (rabbit vs pig), with the mass of hair on a rabbit being greater relative to a pig. Further, the relatively hot and dry conditions during our experiment meant that the upper surface of the carcasses dried quickly, and this would have made the skin more difficult to consume for insects, reducing the mass loss potential over the time frame of our study.

Other factors also contribute to mass loss, including water loss and the action of the microbial community (Pechal et al., 2013). Even with complete insect exclusion, we found approximately 30% of carcass mass was lost over 12 days, demonstrating the importance of these other factors. Indeed, the mass loss regardless of insect activity highlights the complexity of the many interacting microbial and abiotic factors that generate the necrobiome and contribute to the decomposition process (Benbow et al., 2013). Our study joins a suite of others that have demonstrated the critical importance of insects to the carrion decomposition process (Payne, 1965; Peakall et al., 2003; Pechal et al., 2014). We have shown, however, that this essential ecosystem service occurs at similar rates in different microhabitats within the broader grassy woodland ecosystem. This result may not be applicable in very different habitat types (e.g. dense rainforest versus tropical savanna).

Habitat had strong effects on generalist but not specialist insects

We found that the composition of beetle and ant assemblages at carcasses, as well as predators, differed between grassland and tree habitats, but the composition of fly assemblages did not respond to habitat. This agreed with our prediction that vagile and specialist flies would show the weakest response. This finding suggests that different components of the carrion insect community perceive carrion and interact with the surrounding habitat in different ways. Specialist flies view carrion as their habitat and largely ignore the surrounding habitat because finding their next carcass is critical to continuity in their life cycle, and being a good disperser is essential to this. In contrast, ants and beetles contained more dispersal-limited species, as well as a mix of generalist scavengers or predators, and apart from a few known carrion specialists (e.g. *Ptomaphila lacrymosa*, *Creophilus erythrocephalus*), most ants and beetles do not require carrion to complete their life cycle, viewed carrion as an opportunistic resource, and were more responsive to the surrounding habitat. Insects grouped into a broad saprophagous functional group showed a stronger response to habitat than flies, but weaker response than ants or beetles, and this was because they were comprised of both specialist flies as well as some beetles. Predators were comprised of both beetles and ants and so showed a similarly strong response to habitat as these two taxa. Thus, we show that environmental variation occurring over relatively small scales of 100s of metres appears to be important in shaping opportunistic beetle and ant assemblages, but unimportant in shaping specialist or obligate fly assemblages and their critical role in carrion decomposition.

Differences in carrion insect communities between environments are commonly documented (Anderson, 2011; Kavazos & Wallman, 2012), but rarely with a focus on diverse insect communities comprising multiple taxa. Our study also contrasts with others at larger scales, such as that by Farwig et al. (2014) who found that carrion insect assemblages changed in composition along a gradient of altitude and temperature. At such large scales it is not surprising that carrion insect communities differed, as other biogeographic factors come into play such as climate and species physiological requirements (Chown & Gaston, 1999). Temperature differences were minimal between our tree and grassland habitat types (see also Barton et al. 2017), and abiotic factors at the carcasses were unlikely to be driving the differences in insect communities. Rather, our results show that other factors such as resource specialization and dispersal capacity of different taxa or functional groups can interact with habitat variation and lead to different patterns of spatial variation.

Effects of insects on carcass mass loss

We found significant negative effects of fly evenness and ant abundance on carrion mass loss, but no effects of beetles, and limited effects of saprophages or predators. Further, compositional differences in fly assemblages were correlated with differences in carcass mass loss, but this was not shown for any other taxa or functional group. This confirms our prediction that flies would be most likely to have an effect, but also reveals the surprising role of ants in carrion decomposition.

Our study is one of very few that have directly examined the relationship between insect diversity and carrion decomposition. For example, a study by Voss et al (2009) in Western Australia, showed that fewer carrion insect species were found in simplified agricultural land compared with nearby bushland, and that decomposition was also slower in agricultural land. However, they did not collect quantitative data on insects, and their study design meant it was not possible to attribute decomposition rates directly to differences in insect communities. On the other hand, Farwig et al (2014) found an effect of beetle composition on carrion decomposition, particularly reduced decomposition in the absence of larger beetles, thus providing some of the first evidence of insect communities mediating carrion decomposition rate.

Our best models of carcass mass loss also included a negative effect of ant abundance. We observed large numbers of the large meat ant *Iridomyrmex purpureus* on some carcasses, with workers preying on fly larvae and taking them back to their nest. Given the small size of rabbit carcasses, and moderate number of fly larvae, it is feasible that predation of fly larvae by meat ants could inhibit the proliferation of larval masses and therefore decomposition, leading to our result. This is supported, in part, by the finding by De Jong and Hoback (2006) that rat carcasses near nests of *Myrmica sp.* in a field in Colorado, USA, were often overrun with ants, and had lower numbers of fly larvae.

Our results were surprising because higher diversity (i.e. higher species richness or evenness) was not related to greater carrion mass loss. This could be viewed as contrary to biodiversity-ecosystem function dogma that suggests more species lead to improved or more efficient ecological processes (Hooper et al., 2005). In our case, it was more uneven (i.e. less diverse) fly assemblages that was associated with greater mass loss. This indicates that dominance of assemblages by only a few species (in our case *Chrysomya* spp.) leads to greater mass loss, and that these few species are the driving forces behind carrion consumption and mass loss. Of course, it is debatable whether rapid carrion mass loss is actually a desirable ecological outcome, but it is certainly important in driving nutrient flux, which is a key measure in the plant decomposition literature (Handa et al., 2014; Setala & McLean, 2004). The case for insect biodiversity *per se* as being important for decomposition is therefore not supported by our study, rather it is key species that seem to be critical to this particular ecological process.

It is well established that fly larvae are the primary insect consumers of carrion (Payne, 1965), and were the key drivers of carrion mass loss in our experiment. The intense inter-specific competition among flies at carrion (Kouki & Hanski, 1995; Smith & Wall, 1997) means that lower diversity of species could yield higher carrion consumption due to competitive release. This hypothesis could be tested with meso-cosm experiments that controls the mix of fly species present at different carcasses. Such experiments are common in the plant decomposition literature (Handa et al., 2014; Schadler & Brandl, 2005) as well as for dung insect assemblages (Beynon et al., 2012; Lahteenmaki et al., 2015). This could provide further insight into the functional complementarity or redundancy of species at carrion, and differential resource consumption rates under different species mix scenarios. Such knowledge can help to guide understanding of the consequences of species loss or gain for modified landscapes and ecosystem function.

Implications and Conclusions

A motivating question behind this study was how carrion decomposition is maintained in variable environments. We have shown that variable environments lead to differences in parts of the carrion insect community, but not in the rate of the carrion decomposition process. We interpret this as indicating some level of functional complementarity among the generalist ant and beetle assemblages. This particular component of the carrion fauna differed in composition, but not richness or abundance, indicating different species were filling similar functional scavenger or predator roles in each habitat. In contrast, the fly assemblages did not differ among habitat types, indicating a level of redundancy among species when comparing assemblages in this way. Yet, we found important effects of fly evenness and composition on carrion mass loss, demonstrating there was variation in fly assemblages among carcasses that was not explained by broad habitat type, and this may be due to other mechanisms such as inter-specific competition or spatial aggregation.

Our study also raises some questions about how environmental variation in the form of modified landscapes might affect the ecosystem service of carrion decomposition provided by insects. We show it is likely that specialist carrion insects may be resilient to landscape changes that lead to relatively small-scale changes in vegetation cover. Further, given the dominant role of flies in this process, with the bulk of work undertaken by a core set of relatively common species, the potential for landscape change to lead to changes in decomposition rate is likely to be small. Nevertheless, the high sensitivity of generalist or opportunistic insects associated with carrion to environmental variation indicates the impact of landscape change is most likely to be experienced by this more diverse component of the carrion food web.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Map showing the location of our study

Figure S2. Cage structures used to house the rabbit carcasses at each site.

Figure S3. Diagram showing overlap among insect taxa and functional groups examined in this study.

Figure S4. Species accumulation curves for assemblages of flies, beetles, and ants.

Figure S5. Relative proportion of fly species sampled from each rabbit carcass, ranked in order of increasing assemblage evenness.

Table S1. List of insect species collected from rabbit carcasses.

Figure 1. Mean (± se) mass loss of rabbit carcasses with insect access or exclusion, and placed in either grassland or tree habitat types.

Figure 2. Mean (± se) species richness of beetles and predators from carcasses placed in either grassland or tree habitat types.

Figure 3. Principle coordinate analysis ordination plots for assemblages of (a) flies, (b) saprophages, (c) beetles, (d) ants, and (e) predators present at carcasses in grassland or tree habitat types. Lines represent convex hulls around each habitat type, and percentage variation explained is given for each axis.

Figure 4. Linear relationship between carcass mass loss and (a) fly evenness or (b) ant abundance. Dotted lines show 95% confidence intervals.

Figure 5. Linear relationship between pair-wise differences in fly assemblages and carcass mass loss. Dotted lines show 95% confidence intervals.

Table 1. Summary of GLMMs (abundance, species richness) and LMMs (evenness) testing for an effect of habitat type on the abundance or species richness of all species, ants, beetles, flies, predators, and saprophages. Significant effects are shown in bold.

Response variable	Insect group	Wald statistic	d.f.	P
Abundance	Ants	1.640	1	0.236
	Beetles	0.940	1	0.359
	Flies	0.070	1	0.797
	Predators	0.020	1	0.885
	Saprophages	0.010	1	0.935
Species richness	Ants	0.130	1	0.716
	Beetles	10.800	1	**0.011**
	Flies	0.020	1	0.893
	Predators	7.720	1	**0.024**
	Saprophages	0.830	1	0.390
Evenness	Ants	0.850	1	0.384
	Beetles	0.340	1	0.575
	Flies	0.110	1	0.746
	Predators	2.180	1	0.178
	Saprophages	0.020	1	0.893

Table 2. Summary of best models (” AICc<2) of carcass mass loss in response to abundance, species richness, and evenness of (a) flies, beetles, and ants, or (b) predators and saprophages.

(a) Intercept	Ant abundance	Ant species richness	Fly evenness	R^2	df	AICc
1694	-331.6	-	-336.9	0.447	5	252.2
1585	-	-	-370.6	0.302	4	252.5
1736	-	-271.5	-405.8	0.386	5	254.1

(b) Intercept	Predator abundance	Saprophage abundance	Saprophage evenness	R^2	df	AICc
1413	-	-	-	0.000	3	255.6
1284	-	311.4	-	0.116	4	256.8
1530	-279.1	-	-	0.092	4	257.3
1495	-	-	-264.1	0.084	4	257.4

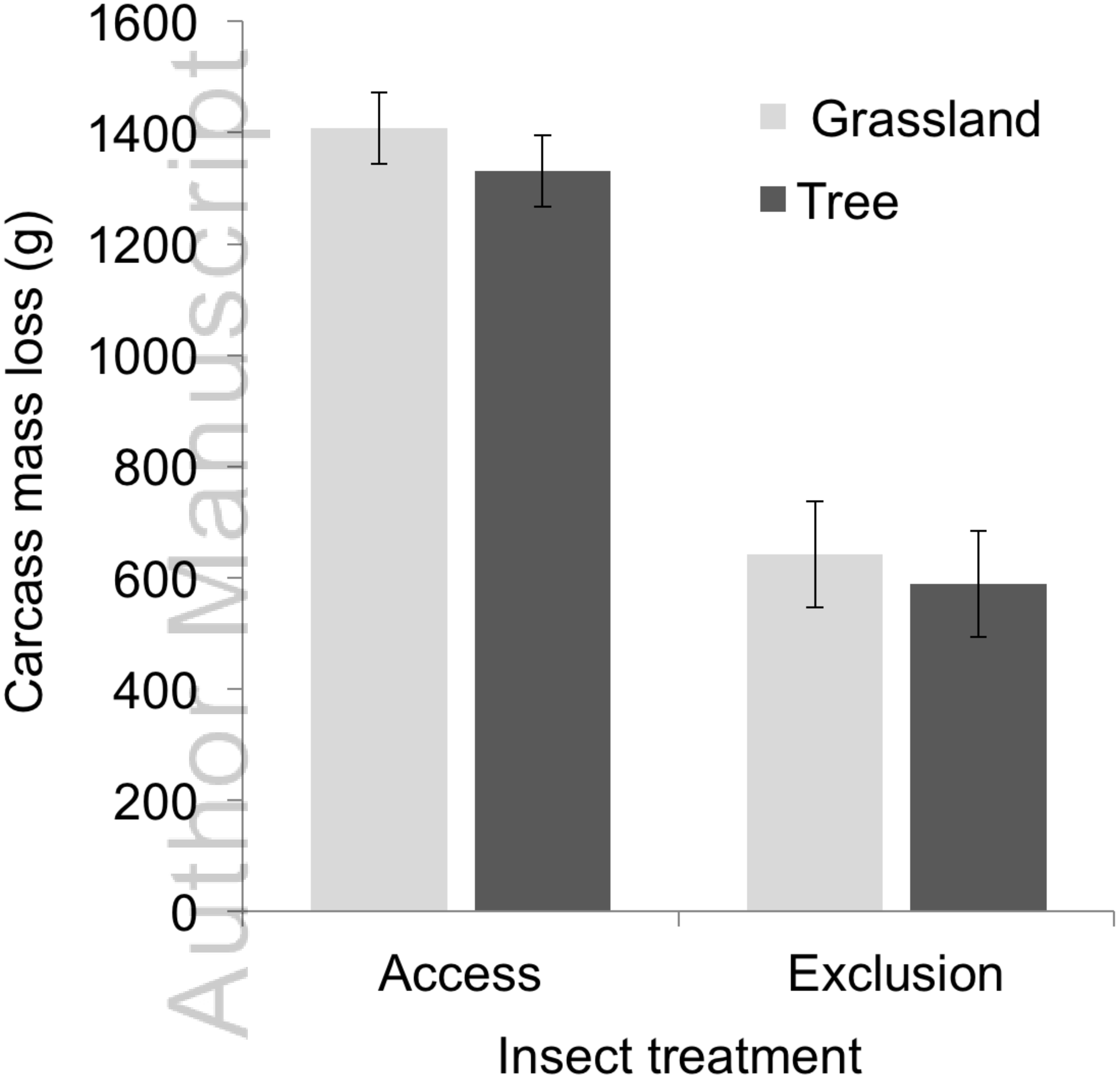
1600
1400
1200
1000
800
600
400
200
0
Carcass mass loss (g)
Grassland
Tree
Access
Exclusion
Insect treatment

Fig1.tiff

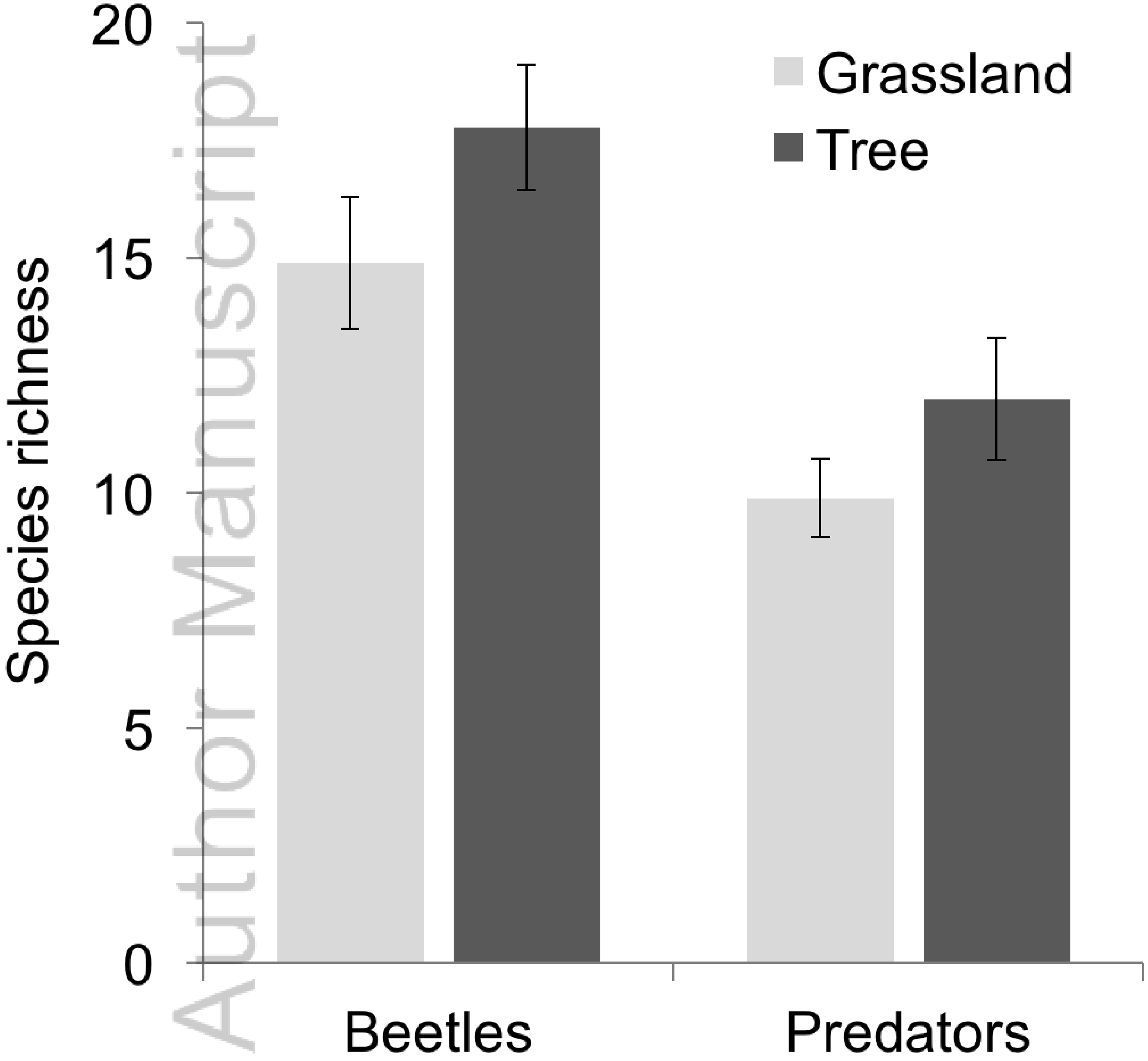
20
15
10
5
0
Species richness
Grassland
Tree
Beetles
Predators

Fig2.tiff

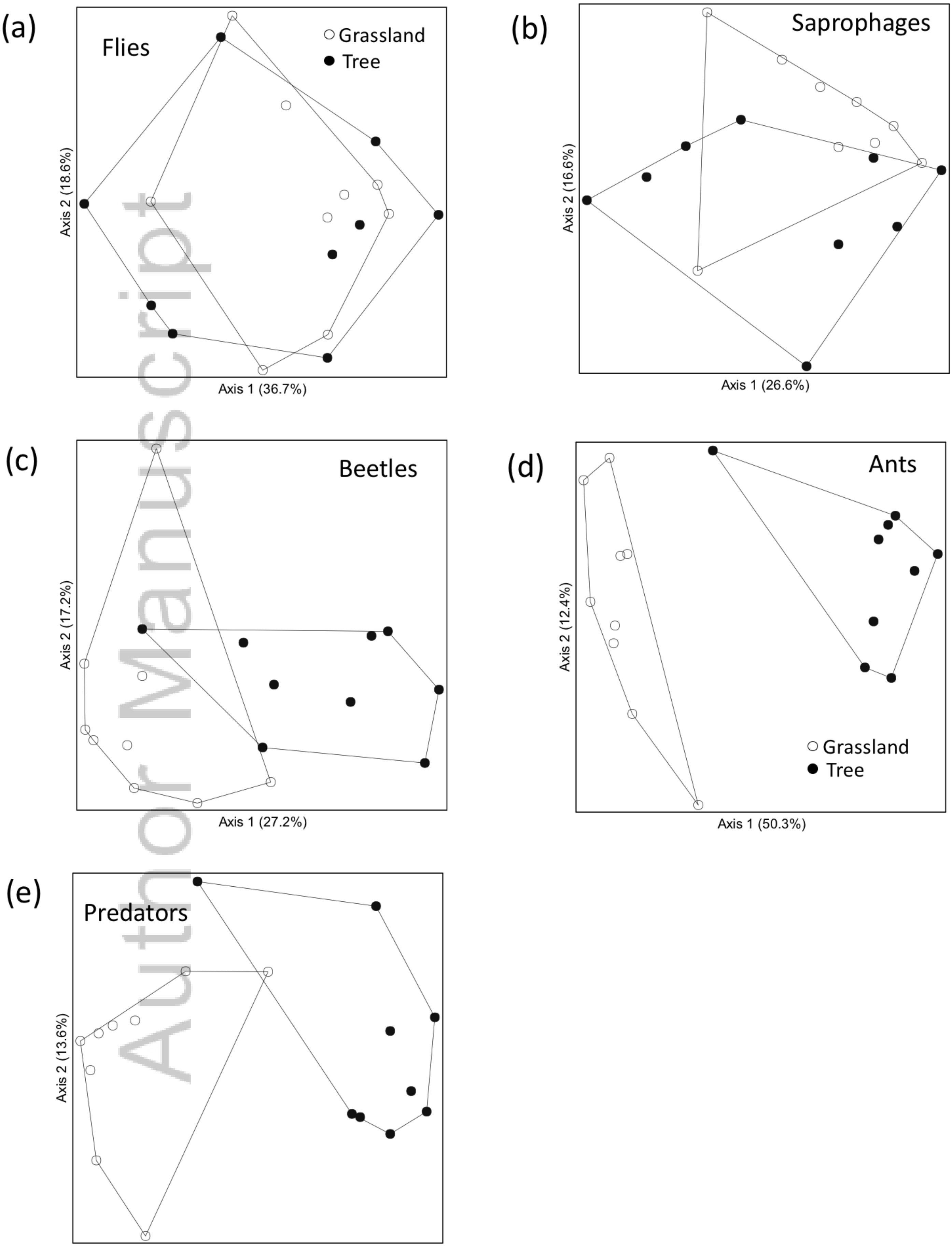
(a)
Flies
Grassland
Tree
Axis 2 (18.6%)
Axis 1 (36.7%)
(b)
Saprophages
Axis 2 (16.6%)
Axis 1 (26.6%)
(c)
Beetles
Axis 2 (17.2%)
Axis 1 (27.2%)
(d)
Ants
Grassland
Tree
Axis 2 (12.4%)
Axis 1 (50.3%)
(e)
Predators
Axis 2 (13.6%)
Axis 1 (49.9%)

Fig3.tiff

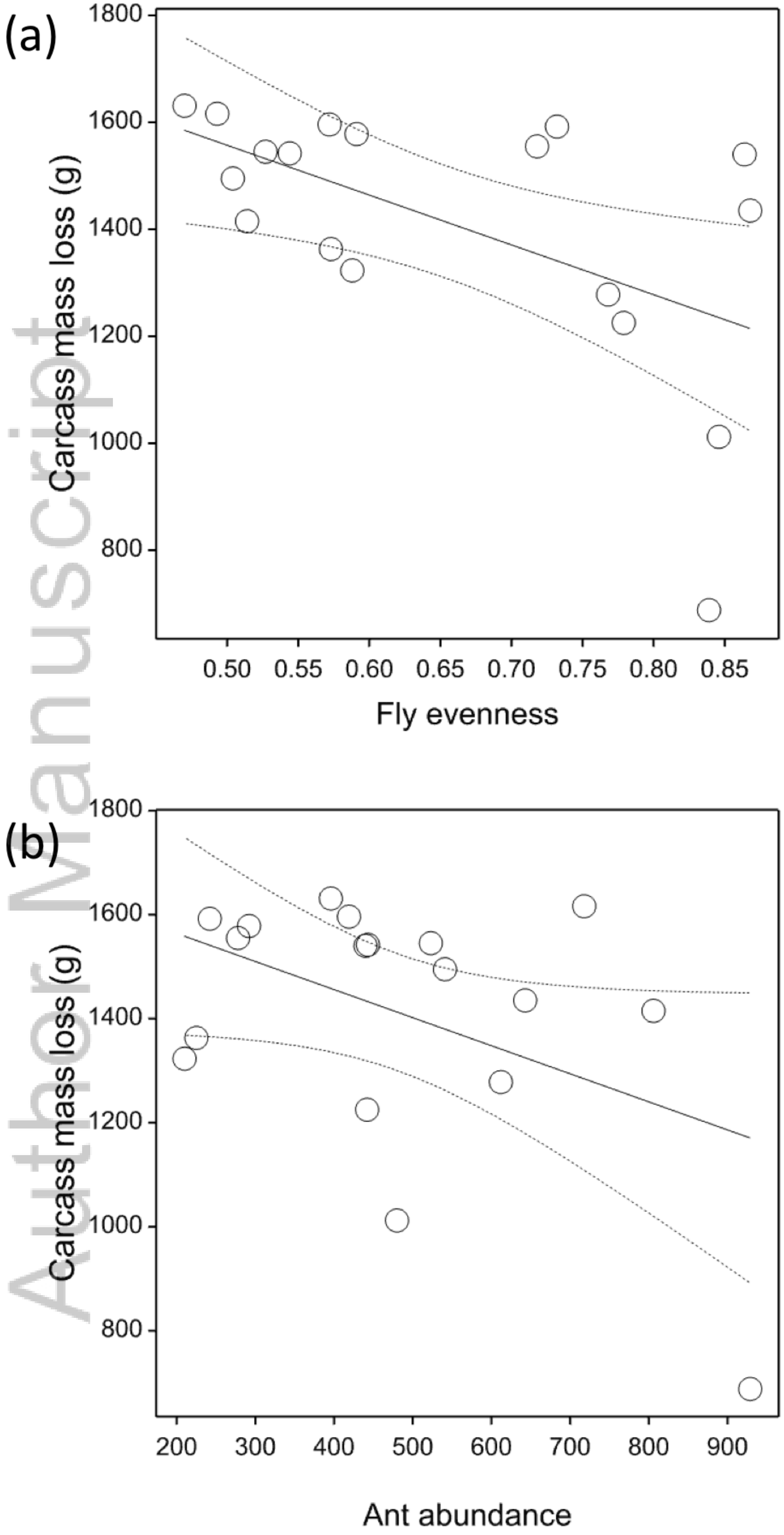
(a)
Carcass mass loss (g)
1800
1600
1400
1200
1000
800
0.50
0.55
0.60
0.65
0.70
0.75
0.80
0.85
Fly evenness
(b)
Carcass mass loss (g)
1800
1600
1400
1200
1000
800
200
300
400
500
600
700
800
900
Ant abundance

Fig4.tiff

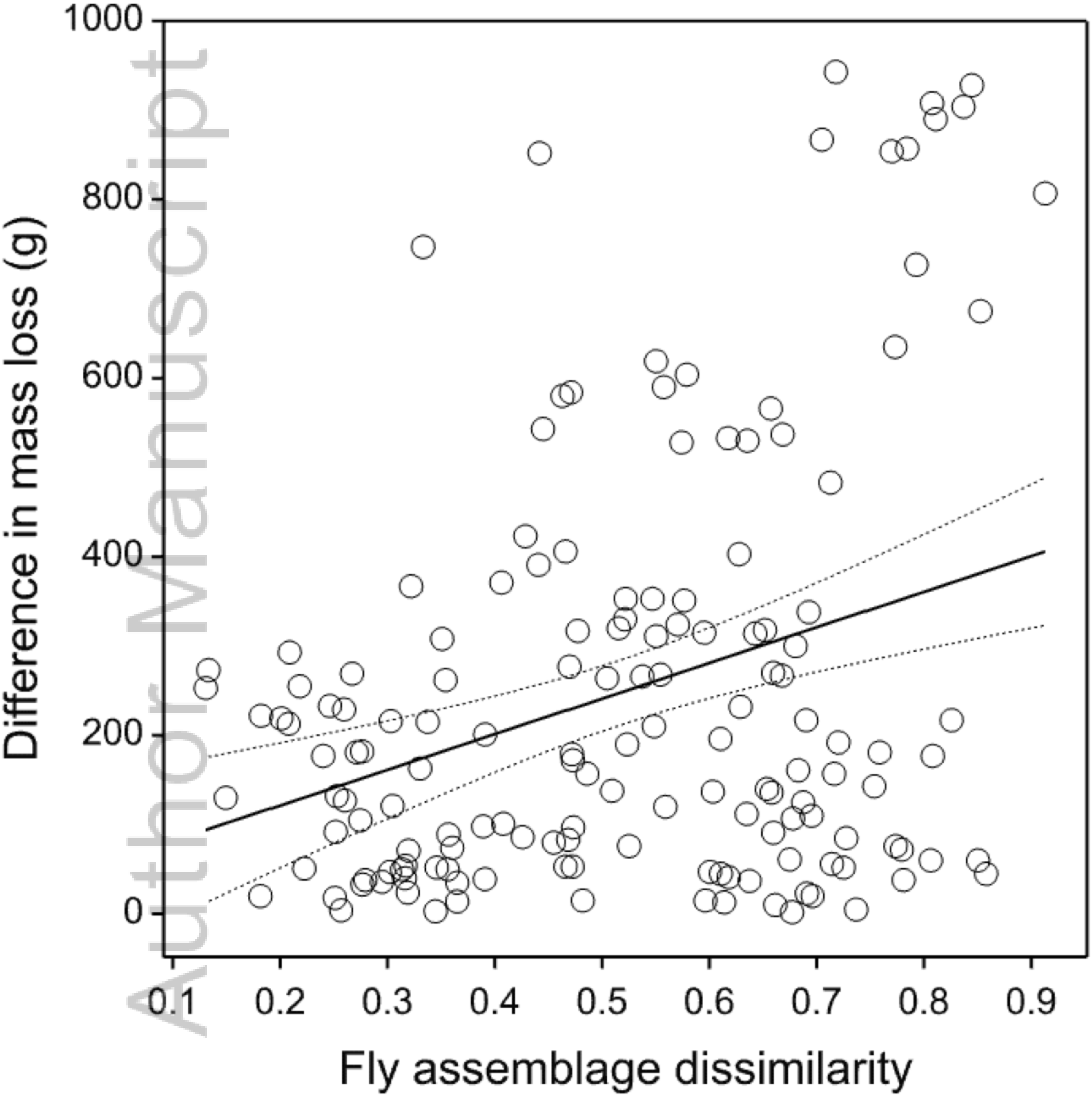
Difference in mass loss (g)
1000
800
600
400
200
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Fly assemblage dissimilarity

Fig5.tiff