



Community Ecology

Drastic changes in ground-dwelling beetle communities following high-intensity deer culling: insights from an island ecosystem

Blake M. Dawson^{1,*}, Maldwyn J. Evans^{2,3}, Philip S. Barton^{3,4}, Masashi Soga^{4,5}, Kahoko Tochigi^{5,6}, Shinsuke Koike^{5,6}

¹School of Environmental and Rural Science, University of New England, Armidale, NSW 2350, Australia, ²Fenner School of Environment and Society, The Australian National University, Canberra, ACT, Australia, ³School of Life and Environmental Sciences, Deakin University, Geelong, Victoria 3216, Australia, ⁴Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi, Bunkyo, Tokyo 113–8657, Japan, ⁵Institute of Global Innovation Research, Tokyo University of Agriculture and Technology, Fuchu, Tokyo 183-8509, Japan ⁶Corresponding author, mail: bdawso22@une.edu.au

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The overabundance of large herbivores can have detrimental effects on the local environment due to overgrazing. Culling is a common management practice implemented globally that can effectively control herbivore populations and allow vegetation communities to recover. However, the broader indirect effects of culling large herbivores remain relatively unknown, particularly on insect species such as ground-dwelling beetles that perform key ecosystem processes such as decomposition. Here we undertook a preliminary investigation to determine how culling sika deer on an island in North Japan impacted ground-beetle community dynamics. We conducted pitfall trapping in July and September in 2012 (before culling) and again in 2019 (after culling). We compared beetle abundance and community composition within 4 beetle families (Carabidae, Scarabaeidae, Geotrupidae, and Silphidae), across seasons and culling treatments. We found each family responded differently to deer culling. Scarabaeidae displayed the greatest decline in abundance after culling. Silphidae also had reduced abundance but to a lesser extent compared to Scarabaeidae. Carabidae had both higher and lower abundance after culling, depending on the season. We found beetle community composition differed between culling and season, but seasonal variability was reduced after culling. Overall, the culling of large herbivores resulted in a reduction of ground-dwelling beetle populations, particularly necrophagous species dependent on dung and carrion for survival. Our preliminary research highlights the need for long-term and large-scale experiments to understand the indirect ecological implications of culling programs on ecosystem processes.

Key words: ecosystem processes, necrobiome, Carabidae, Scarabaeidae, sika deer, Silphidae

Introduction

The overabundance of large herbivore species is a global problem (Côté et al. 2004, Gordon et al. 2004), which can cause detrimental effects on ecosystems (Barton et al. 2011, Gerhardt et al. 2013, Iida et al. 2016). For example, in Japan, deer overabundance has resulted in the loss of understorey vegetation and associated wildlife, soil erosion, and hindrance to forest regeneration (Côté et al. 2004), while in Australia the overabundance of kangaroos has had detrimental effects on plant communities (Gordon et al. 2021). Overabundant species can alter landscapes by consuming vegetation and degrading

plant communities by limiting regrowth and dispersal processes (Côté et al. 2004, Velamazán et al. 2017). In some situations, overconsumption and selective foraging can alter the plant community composition and lead to local extinctions, as floral species that are not favored by the herbivore species gain a competitive edge (Akashi and Nakashizuka 1999, Gill and Beardall 2001, Gorchov et al. 2021). Moreover, the disturbance of plant communities by large herbivores can have cascading effects on habitat structure and its dependent fauna and food webs (Den Herder et al. 2004, Foster et al. 2014, Mahon et al. 2020). It can impact water, nutrient, and carbon

cycling, and increase the susceptibility of the environment to exotic species invading (Eschtruth and Battles 2009, Beguin et al. 2011, Cardinal et al. 2012, Seki and Koganezawa 2013).

A common management practice to address herbivore overpopulation is to implement translocation or controlled culling programs (Putman et al. 2011, Driscoll et al. 2019, Ikeda et al. 2019). The goal of such programs is to reduce herbivore numbers to a desired level that reduces the ecological impacts of the species (Tanentzap et al. 2012, Enoki et al. 2016). Culling and associated permitted hunting also provides economic benefits when culled species are removed from the environment and used for human or pet food for commercial gain (Nugent and Choquenot 2004). Despite the often-negative perception of culling by the public (Sharp et al. 2011), research on the management practice has been shown to be ecologically effective and has been implemented globally, targeting a wide range of species such as deer (Wäber et al. 2013), boars (Croft et al. 2020), and kangaroos (Gordon et al. 2021).

While the negative effects of overabundant large herbivores are well established, there is a need to understand how the culling of herbivores might impact key ecological processes. If herbivore numbers are reduced, for example, any potential benefits that culling provides could be impacted (Bardgett and Wardle 2003, Foster et al. 2014). Decomposer and scavenger communities depend on the carcass remains of large herbivores as a food resource and breeding substrate, while other decomposer species depend on dung for survival (Nichols et al. 2008, Butterworth et al. 2022). These decomposers play a key role in maintaining biodiversity and ecosystem functions and services such as nutrient and energy cycling (Barton et al. 2013, Englmeier et al. 2022). The sudden removal of a large number of herbivore species from an ecosystem may have unintended negative consequences on dependent species, which in turn could have bottom-up effects on the food web and broader ecosystem function (Iida et al. 2016). Further research on the effects of culling of herbivores as a management tool is required to determine how ecosystems might respond.

Nakajima Island in Japan offers a unique opportunity to study the effects of herbivore culling on biodiversity and ecosystems. Since the introduction of sika deer (*Cervus nippon* Temminck) to the island, the understorey vegetation has been under increased pressure due to high deer density (Yama et al. 2019). In an effort to mitigate the negative ecological impacts of the deer population, a controlled culling program was implemented on the island resulting in a drastic reduction in deer numbers (Ikeda et al. 2019). The island presents an ideal study system for examining the indirect effects of deer culling on ground-dwelling beetle communities in a natural environment without the risk of reintroduction of deer.

In this study, we investigated how ground-dwelling carabid (Carabidae), dung (Scarabaeidae, Geotrupidae), and carrion (Silphidae) beetles responded to a reduction in deer population on Nakajima Island, Japan. We focused on these beetles because of their clear role in ecosystem processes as predators and scavengers, and are likely dependent, in part, on large herbivores as a food resource and breeding substrate. We discuss our results in light of the effects of deer culling on the beetle community and how this may indirectly influence key ecological processes. This research will help to provide insight into the broader impacts of culling programs on ecosystems and the potential consequences for dependent species.

Materials and Methods

Study Site

We conducted our study on Nakajima Island (42°36' N, 140°51' E), which is centrally located within Lake Toya, at an approximate

distance of 4 km from the lake. The snow-free period on the island spans from April to November. The majority of the island is covered by natural, broad-leaved forests, which consist of species like *Acer pictum* Thunb. subsp. *momo* H. Ohashi and *Tilia japonica* Simonk var. *japonica* Miq. Sika deer were introduced to the island in 1957–1966 and have since experienced a rapid increase in population, reaching a peak of 50 deer/km² in response to a prohibition of hunting and the absence of natural predators (Ikeda et al. 2013). A controlled culling program was implemented in 2012 to reduce deer numbers, resulting in a deer density of roughly 12 deer/km² in 2019 (Kaji and Takeshita 2022). Further information about the island ecology and deer populations are detailed in Ikeda et al. (2015) and Kaji et al. (2005).

Beetle Sampling

We conducted two rounds of ground beetle community sampling on the island in 2012 (prior to culling) and 2019 (after culling). To capture beetles when they were most active in this region, we conducted sampling twice in each sampling year, once in July and again in September. We established 30 sampling plots along a 3 km transect, spaced 100 m apart from each other (only 10 sites in July 2012). The transect ran through the center of the island from the east to the west coast. We deployed a single pitfall trap, baited with cattle dung and fermented milk to each plot. Dung and fermented milk were used as they are known to attract ground-dwelling beetles (Suttiprapan and Nakamura 2007). We constructed the pitfall traps using plastic containers (22.5 cm diameter, 26.6 cm depth) and plastic cups (8.3 cm diameter, 11.5 cm depth). To set a trap, we buried a plastic container filled with fermented milk into the ground, ensuring the rim was level with the ground. We hung the plastic cup containing dung inside the container using wires. We also placed a plastic roof over the trap to protect it from rain and leaves. We left the traps in place for a period of 3 days, after which we counted and collected all the beetles. We identified them as the highest taxonomic unit possible using morphological characteristics (Ueno et al. 1985).

Data Analysis

To investigate the effect of deer culling on beetle populations and community composition, we performed 3 statistical analyses. First, we analyzed the response of the beetle community composition to deer culling and performed a permutational multivariate analysis of variance test (PERMANOVA) using the Vegan package (Oksanen et al. 2022) in R (R Core Team 2023). We used the interaction of month and culling as fixed effects, and site as a random effect. We used a Bray–Curtis dissimilarity matrix to calculate the distance matrices. To visualize the beetle communities, we plotted the ordination as a non-metric multidimensional scaling (NMDS) plot. We also calculated Pielou's evenness for each combination of month and culling to identify changes in overall relative abundances using the Vegan package (Oksanen et al. 2022).

Second, we conducted generalized linear mixed modeling (GLMM) to determine how the interaction of month (July and September), culling (before culling and after culling), and family (Carabidae, Scarabaeidae, Geotrupidae, and Silphidae) influenced beetle abundance. To control the effects of repeated measures, we included the site as a random effect. We fit a GLMM using the glmmTMB package in R, assuming a Poisson error distribution and a log-link function (Brooks et al. 2017). We then conducted pairwise comparisons of the predicted variables using the emmeans package (Lenth 2023), and assessed model performance using the performance package (Lüdtke et al. 2021).

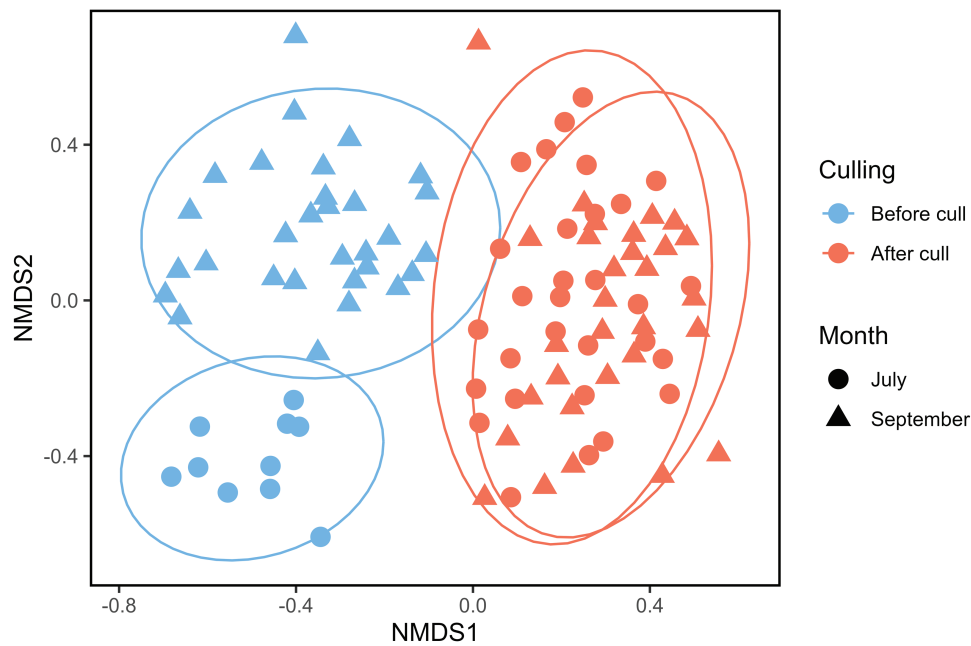


Fig. 1. NMDS plot of beetle abundance community composition comparing July (circle) and September (triangle), before (blue) and after (red) culling.

Finally, to understand how deer culling influenced individual beetle species, we conducted a Bayesian ordination and regression analysis using the Boral package (Hui 2016). We assumed a negative binomial distribution and 2 latent variables and used the same interaction and random effect as the PERMANOVA. We grouped the beetle species by family and plotted the X-coefficient estimates as effect sizes. We interpreted the effects as significant if their 95% credible intervals did not cross the zero-effect posterior median line. All statistical analyses were performed in R version 4.2.3 and the plots were created using the ggplot2 package (Wickham 2016).

Results

In total, we collected 24 species from 4 beetle families (Carabidae, Scarabaeidae, Geotrupidae, and Silphidae). We found a significant interactive effect of culling and month on the beetle community composition (PERMANOVA: $F = 14.739$, $P < 0.001$). Distinct beetle communities were present in July and September before culling, but these communities became similar after culling (Fig. 1). We found the beetle communities were more even in July and September after culling compared to before culling (Table 1).

We found beetle families responded differently to culling and month (Fig. 2). Scarabaeidae had the largest loss in abundance after culling, but also displayed significantly reduced abundance in July compared to September, with this significant difference continuing after culling. Silphidae also had a significant reduction in abundance after culling, while culling had no effect on Geotrupidae abundance. Carabidae displayed mixed results, with culling causing both an increase and decrease in abundance, depending on the month.

The multispecies Bayesian analysis revealed that only 2 species of Scarabaeidae had a significantly higher abundance in September compared to July (Fig. 3), while the remaining species of all families were evenly split between having a significantly higher abundance in July or no significant difference between seasons. For the culling effect, generally, the species that were significantly more abundant in July had a significantly higher abundance before culling than after culling. No species had a significantly higher abundance after the

Table 1. Pielou's evenness values for July and September before and after culling.

	July	September
Before cull	0.801	0.610
After cull	0.919	0.876

culling. Almost all Scarabaeidae species were significantly affected by the culling event, experiencing a reduction in abundance. Only some species had a significant interaction effect of both month and culling (see Supplementary Figure S1).

Discussion

We investigated the effects of deer culling on ground-dwelling beetles in a unique island ecosystem. Our results suggest that the beetle community differed clearly between seasons, but after culling this seasonal difference was reduced. We also found that culling significantly reduced beetle abundance, but this was dependent on the beetle family and month. We found beetle community evenness increased after culling. Furthermore, we showed that approximately half of the beetle species we examined were impacted by culling, whereas the remaining species showed little change in abundance after culling. Notably, there were no beetle species that were higher in abundance after culling. Our study demonstrates a plausible link between ground-dwelling beetles and large herbivores on an island ecosystem and suggests there may be important ecological ramifications of reduced herbivore populations.

Each beetle family responded differently to the reduction of large herbivores. Scarabaeidae displayed the most dramatic loss in abundance after culling, which is likely linked to their dependence on dung as a food resource and breeding substrate (Nichols et al. 2009). Dung is generally a temporally consistent ephemeral resource, but with the loss in herbivore numbers on the island, dung availability was likely reduced (Butterworth et al. 2022). Therefore, species that are dependent on dung would be negatively affected. Silphidae also displayed a loss

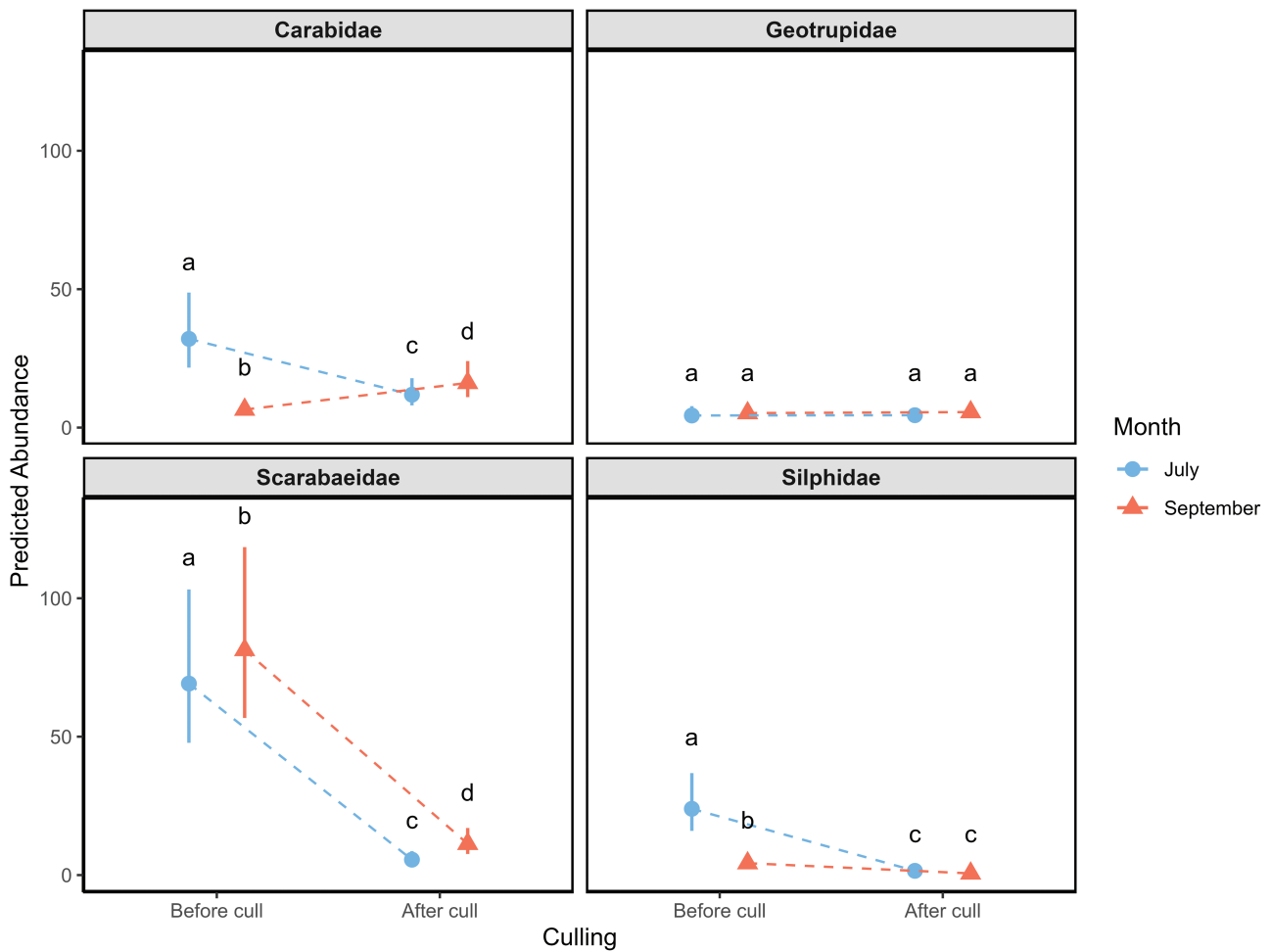


Fig. 2. Predicted abundance of beetle community in July (blue) and September (red), and before and after deer culling, for each beetle family. Predicted abundances derived from GLMMs. Significance within each family is denoted by different letters ($P < 0.05$). Error bars represent 95% confidence intervals.

in abundance after culling, but to a lesser extent than Scarabaeidae. Silphidae are carrion beetles that are dependent on carrion for survival and reproduction, therefore the reduction in carcass availability due to the removal of herbivores from the ecosystem would directly impact Silphidae abundance (Holloway and Schnell 1997, Dekeirsschieter et al. 2011). Carrion is a patchy and unpredictable ephemeral resource, and those species dependent on carrion often have fluctuating populations, depending on carrion availability (Barton et al. 2019, Butterworth et al. 2022). This resource scarcity, potentially due to different deer mortality rates between seasons, is the likely reason for the seasonal variation in Silphidae abundance before culling observed in our study. Lastly, Carabidae both increased and decreased in abundance after culling, depending on the season. Carabidae are generally predators, though the family does occupy a wide range of ecological niches (Lövei and Sunderland 1996, Kotze et al. 2011). Some species of Carabidae are likely indirectly linked to herbivore populations due to changes in habitat structure due to herbivore grazing patterns (Ings and Hartley 1999). In our study system, the understorey vegetation has been diminished due to overgrazing (Yama et al. 2019). As herbivore numbers are reduced from culling, vegetation would recover (Donlan et al. 2002), thereby altering Carabidae habitat and prey abundance, resulting in mixed effects on Carabidae populations, depending on the individual species ecological niche.

Our study shows changes in the abundance of key groups of ground-dwelling beetles, most of which contribute to decomposition

processes (Scarabaeidae, Geotrupidae, and Silphidae) (Nichols et al. 2009). The beetle communities became more even after culling, likely due to the reduction in abundance of the most dominant species. With the reduction of beetles following the culling of deer, there could be implications for the rate or efficiency of dung or carcass consumption and resulting nutrient turnover and dispersal pathways. It might also be that a broader suite of insects than assessed in this study could be impacted by the removal of large herbivores, such as flies and other insect species closely linked to decomposition (Braack 1987, Barton and Bump 2019, Benbow et al. 2019). We suggest that ongoing monitoring of populations of necrophagous species and necromass availability is needed to determine the longer-term effects of deer culling on the beetle community and their ecosystem services.

This study was limited to comparing only 1 year before and after the culling event, making it challenging to disentangle the effects of yearly variation (or other environmental variables) from the direct impact of culling. The study was also limited by the lack of a control as the whole island was subjected to the culling program. However, despite these limitations, this study still provides useful insight into the possible indirect effects of culling. To gain a comprehensive understanding of the long-term effects of culling, future research should encompass multiple years both before and after culling, as well as incorporate controls into the experimental design. This approach will enable the incorporation of yearly variations and facilitate a more accurate assessment of the communities' ability to

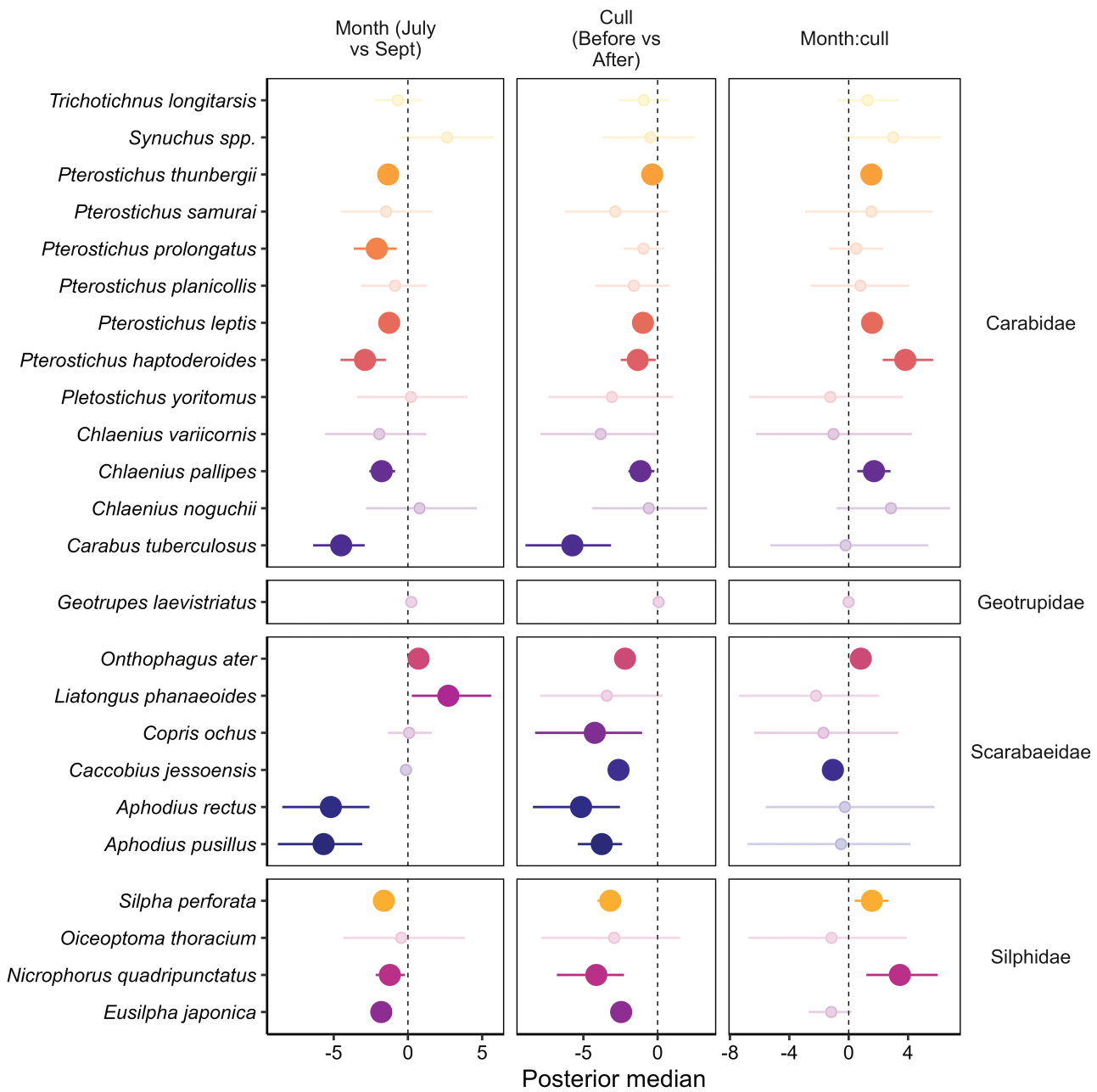


Fig. 3. Bayesian ordination and regression analysis results of effect of season and cull on abundance of each beetle species. Credible intervals (95%) which do not cross the zero posterior median and displayed as not faded are significant. If significant (not faded), the side of the posterior median where the dot falls represent the direction of significance (e.g., for month, dots on the left that are not faded mean species had a significantly higher abundance in July compared to September). Species are grouped by family membership.

return to equilibrium after culling (Gordon et al. 2004). In particular, a more long-term approach may be able to identify if the reduction of the targeted herbivore leads to the eventual increase of herbivores that may have originally been competitively excluded.

While we observed the effects of deer culling on the abundance and composition of ground-dwelling beetles, it is probable that the extent of these changes depends on the intensity of culling. In our study system, there was a relatively high level of deer culling, which can be attributed to the clear results obtained. From a management standpoint, it is crucial to understand the degree to which changes in insect fauna can vary based on the level of culling, as well as to determine if there exists a threshold beyond which the loss of beetles will sharply escalate.

Our study emphasizes the need to understand comprehensively both the direct and indirect ecological impacts associated with reducing large herbivore species in an ecosystem. While culling can be an effective management tool to mitigate the effects of overabundant herbivores, future culling programs should carefully consider the complex ecological interactions between herbivore species and the broader ecosystem. By doing so, we can ensure the preservation of key ecological processes and maintain the integrity of food webs.

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Author Contributions

Blake Dawson (Formal analysis [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Maldwyn Evans (Formal analysis [equal], Visualization [equal], Writing—review & editing [equal]), Philip Barton (Formal analysis [equal], Visualization [equal], Writing—review & editing [equal]), Masashi Soga (Formal analysis [equal], Methodology [equal], Visualization [equal], Writing—review & editing [equal]), Kahoko Tochigi (Methodology [equal], Writing—review & editing [equal]), and Shinsuke Koike (Methodology [equal], Writing—review & editing [equal])

Supplementary Material

Supplementary material is available at *Environmental Entomology* online.

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