Response of grassland insect diversity and assemblages to the invasive Gleditsia triacanthos in South Africa

Thandeka Mahlobo

thandekatee99@gmail.com

University of the Free State

Caswell Munyai

University of KwaZulu-Natal

Grant Martin

Rhodes University

Nontembeko Dube

University of the Free State

Research Article

Keywords: Invasion, honey locust, ground-dwelling insects, grassland, community structure

Posted Date: July 15th, 2025

DOI: https://doi.org/10.21203/rs.3.rs-7026506/v1

Additional Declarations: No competing interests reported.

Abstract

Invasive alien tree species alter open grassland ecosystems by introducing shading and vertical structure, which can modify habitat conditions and influence insect community composition and dynamics. *Gleditsia triacanthos*, a rapidly spreading invasive alien tree, is transforming grasslands in South Africa. This study assessed the impact of *G. triacanthos* on terrestrial insect groups, focusing on Hymenoptera (ants), Coleoptera (beetles), Orthoptera (locusts and grasshoppers) and Blattodea (cockroaches and termites). Insects were collected using pitfall traps in five paired (invaded and uninvaded) grassland locations in the Free State province, over four seasons. A total of 19,629 individual insects from four orders, belonging to 34 families and 147 species or morphospecies, were identified across all sites and seasons. Hymenoptera exhibited the highest abundance, whereas Coleoptera had the highest species richness. Insect community composition was significantly affected by invasion and season. Uninvaded sites had higher species abundances and lower dominance, with peaks occurring in summer and declines in winter. However, Blattodea and some ant genera (*Pheidole*, *Anoplolepis*, and *Camponotus*) were more abundant under *G. triacanthos*. These shifts in insect communities may disrupt processes such as herbivory, soil aeration and decomposition performed by the studied insect groups, and this potentially triggers cascading effects on higher trophic groups and, ultimately, grassland productivity and function through modification of species interactions. Given the rapid spread of *G. triacanthos*, our findings emphasise the need for continued monitoring of *G. triacanthos* spread and its ecological consequences on grassland ecosystems in South Africa.

Introduction

Biological invasions are significant drivers of environmental change (Linders et al. 2019; van Wilgen et al. 2020). Invasive alien plants, a substantial component of these invasions, disrupt biodiversity and ecosystem services (Garcia and Crusella-Trullas 2017; Rai and Singh 2020). They alter habitat quality, reduce species diversity, and affect food sources across trophic levels (Litt et al. 2014). These invasive plants also disrupt the relationships between native organisms, shifting functional niches and compromising ecosystem function and stability (Linders et al. 2019).

The South African Grassland biome, a biodiversity hotspot, supports rare and threatened taxa (Prinsloo et al. 2021). Invasive alien trees modify the structure and complexity of grasslands; they also create microclimates that limit the ability of various fauna to thermoregulate and hydro-regulate (Litt et al. 2014; Garcia and Crusella-Trullas 2017; Galle et al. 2023). They can also alter soil nutrients and reduce native grassland diversity (e.g., Yapi et al. 2018; Lusizi et al. 2024), thus disrupting foraging and reproduction by reducing plant hosts and available food resources (Garcia and Crusella-Trullas 2017; Yapi et al. 2018). Several invasive species are transforming South African temperate grasslands, particularly the high-elevation grasslands. These include *Robinia pseudoacacia* L. (Fabaceae), *Pyracantha angustifolia* (Franch.) C.K. Schneid. (Rosaceae), *Rubus* sect. *cuneifolii* L.H. Bailey (Rosaceae), *Rosa rubiginosa* L. (Rosaceae), *Salix babylonica* L. (Salicaceae) and *Gleditsia triacanthos* L. (Fabaceae) (Martin 2021).

Gleditsia triacanthos (L) (Fabaceae) is a deciduous tree native to central and northern America (Blair 1990) and is a 1b invasive species in South Africa under the NEMBA regulations. The tree spreads rapidly, transforming and degrading grasslands (Henderson and Wilson 2017; Martin 2021). Where invasive, *G. triacanthos* outcompetes indigenous trees, smothers grass species, and its spines injure people and livestock, even after the plant has died (Fernandez et al. 2017). In Argentina's Pampean streams, the tree reduced macrophytes, and this alteration disrupts the aquatic ecosystem, as macrophytes provide critical shelter, breeding grounds, and food sources for a range of organisms (Vilches et al. 2020).

This response of invertebrates, particularly insects, to invasive trees like *G. triacanthos* varies depending on species and the ecosystem it invades. In general, invasive trees alter habitat structure by outcompeting native plants, modifying resource availability and creating novel microclimates, all of which can influence insect communities (Chikowore et al. 2021; Malongweni et al. 2025). Several studies report a decline in insect species diversity in response to invasive alien plants (e.g. Rodriguez et al. 2020; Chikowore et al. 2021). However, not all insect groups respond in the same way; some generalist insects may adapt and exploit new resources and increase in abundance (e.g. Montesinos et al. 2016; Rodriguez et al. 2019).

Given the rapid spread of *Gleditsia triacanthos* in South African grasslands, this study aimed to assess its impact on grassland insect diversity, abundance and community assemblage. Specifically, the study focused on how ground-dwelling insect communities, particularly insects from the orders Hymenoptera (ants), Coleoptera (beetles), Blattodea (cockroaches and termites), and Orthoptera (grasshoppers and locusts), exhibit differences between areas invaded by *Gleditsia triacanthos* and adjacent uninvaded grasslands, with these patterns potentially influenced by seasonal variations..

These insect groups were chosen because they are key components of grassland arthropod communities and play critical ecological roles: ants contribute to soil turnover, predation and seed dispersal (Almedia et al. 2019), beetles aid in nutrient cycling and predation (Maldonado et al. 2019; Alekseev et al. 2024), cockroaches and termites are involved in decomposition, nutrient cycling and soil formation (Jouquet et al. 2011; Enebe and Erasmus 2024), and locusts and grasshoppers in herbivory (Belovsky and Slade 2018; Laws et al. 2018). Their small size and sensitivity to environmental change make them useful indicators for understanding how invasions can affect biodiversity and, in turn, grassland processes and functioning (Gerlach et al. 2013; Solascasas et al. 2022).

Materials and Methods

Site description

This study was conducted at the grassland biome of the Free State Province, South Africa, at the exact locations described by Mahlobo et al. (2025). Specifically, five grassland sites with a well-established *G. triacanthos* invasion, each paired with an uninvaded grassland, were selected in Bloemfontein (Willows

and R700 located ~ 10km apart), near Clarens (Clarens 1 and Clarens 2, also located more than 10km apart from each other), and one in Kroonstad (Kroonstad) (Fig. 1).

Vegetation in the uninvaded grasslands was primarily composed of native grasses. At R700, both Clarens sites and Kroonstad, *Themeda triandra* Forssk (Poaceae) and *Eragrostis lehmanniana* Nees (Poaceae) were dominant, while *Cenchrus clandestinus* Hochst. ex Chiov (Poaceae) was the main grass species present at the Willows site. Although some forb species occurred across these uninvaded areas, they were generally sparse and not ecologically dominant. In contrast, the invaded sites were characterised by dense stands of *G. triacanthos* trees and a few ruderal plant species (Mahlobo et al. 2025).

Insect sampling

Insect communities in the invaded and uninvaded sites were sampled over four seasons (autumn, winter, spring and summer). Only Hymenoptera (ants), Coleoptera (beetles), Orthoptera (locusts and grasshoppers) and Blattodea (cockroaches and termites) were considered in the current study. Sampling was conducted in stands of *Gleditsia triacanthos* and adjacent uninvaded grasslands, located > 10m apart. At each site, pitfall traps were arranged along two transects containing 10 traps. Traps were spaced 5 meters apart within each transect, and the two transects were separated by 10 meters. The traps were 300 ml plastic containers buried with their rims flush with the soil surface. Each trap was filled with 100 ml of ethanediol, chosen for its effectiveness in preserving arthropods without rapid evaporation (Kwon et al. 2022). These were left open in the field for seven days.

Traps were emptied in the laboratory, and insect specimens collected were preserved in 70% ethanol. Ant specimens were identified at the species level whenever possible. Otherwise, all were identified to genus level using Fisher and Bolton (2016), and the species not identified were assigned to morphospecies. Other insect groups were identified to the lowest level possible, mainly using Picker et al. (2019).

Data analysis

Non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity coefficient was used to illustrate how arthropod communities differed between invaded and uninvaded sites at each sampling location. The effects of site (invaded vs uninvaded) and season were assessed using two-way PERMANOVA, and the observed differences in arthropod communities were further examined using the R-value from an Analysis of Similarity (ANOSIM). Similarity Percentage (SIMPER) was also used to identify the species that contributed most to the dissimilarity matrix. Diversity indices, including species richness (S), Simpson’s Diversity Index (1–D), Shannon’s Index (H'), and Dominance, were calculated to compare insect community dynamics between invaded and uninvaded grasslands. Differences in these indices were tested using a paired t-test. Differences in the abundances of each order were tested using a two-way ANOVA, with invasion status and season as fixed factors.

Since location had a significant effect on community composition, each location was analysed separately by comparing invaded and uninvaded sites, and locations were not compared to each other. Prior to the analyses, data were log transformed (i.e. log10 (n + 1) to reduce the dominance of highly abundant species and minimise the impact of extreme values, stabilising variance across the dataset. All analyses were performed using PAST software version 4.03 (Hammer et al. 2001).

Results

A total of 19,629 individual insects from four orders, belonging to 34 families and 147 species or morphospecies, were identified across all sites and seasons. Coleoptera was the most speciose order, representing ~ 50% of total species, followed by Hymenoptera with 35%. Blattodea was the least speciose, representing 6.8% of the total species (Appendix 1). Hymenoptera was also the most abundant order, representing 93.2% of the sampled insects.

Non-metric multidimensional scaling (NMDS) of the arthropod communities revealed distinct differences in community composition between *G. triacanthos*-invaded and uninvaded grasslands, a pattern observed across all sampled locations (Fig. 2). Two-way ANOSIM further confirmed significant differences in arthropod community composition between sites, with high R values indicating strong dissimilarity for Willows ($R = 0.69$, $p = 0.04$), R700 ($R = 0.69$, $p = 0.03$), Clarens 1 ($R = 0.44$, $p = 0.03$), Clarens 2 ($R = 0.56$, $p = 0.01$), and Kroonstad ($R = 0.93$, $p = 0.01$), and across seasons for Willows ($R = 0.68$, $p < 0.001$), R700 ($R = 0.80$, $p < 0.001$), Clarens 1 ($R = 0.56$, $p = 0.004$), Clarens 2 ($R = 0.57$, $p < 0.001$), and Kroonstad ($R = 0.99$, $p < 0.001$). Complementing this, two-way PERMANOVA revealed significant differences in arthropod communities both between sites (Willows: $p < 0.001$; R700: $p < 0.001$; Clarens 1: $p = 0.004$; Clarens 2: $p < 0.001$; Kroonstad: $p < 0.001$) and across seasons (Willows: $p < 0.001$; R700: $p < 0.001$; Clarens 1: $p < 0.001$; Clarens 2: $p < 0.001$; Kroonstad: $p < 0.001$). However, the interaction effect was only significant at Willows ($p = 0.005$), Clarens 2 ($p = 0.01$), and Kroonstad ($p < 0.001$).

Similarity Percentage (SIMPER) indicated that ants (Hymenoptera: Formicidae) contributed most to differences between the invaded and uninvaded sites, with dissimilarity > 60% across the sampled locations (Table 1). At Willows and R700, an ant species, *Pheidole megacephala* (Fibricius), was one of the top contributors and had higher abundances in the invaded grassland. Undescribed ant species, *Pheidole* sp. 01 and *Monomorium* sp. 01, also contributed more at these locations, but were more abundant in the uninvaded grasslands. In Clarens 1, ant species *Anoplolepis custodiens* (Smith) dominated invaded sites, and was a key contributor to the differences. Other key contributors were ant species *Leptogenys* cf *intermedia* and *Monomorium* sp. 01, also abundant under *G. triacanthos*. *Anoplolepis custodiens* and *L*. cf *intermedia* were also key contributors in Clarens 2, but *Tenebrio* sp. 01, abundant under *G. triacanthos*, was a top contributor in this location (Table 1). In Kroonstad, two ant species, *Tetramorium sericeiventre* (Emery) and *Tetramorium* sp. 01 (*setigerum* gp), were the main contributors and were more abundant in the uninvaded grasslands. They were followed by an ant species, *Camponotus cintellus* (Roger), which was more abundant under *G. triacanthos.*

Table 1
SIMPER analysis results showing average dissimilarity in arthropod communities between *G. triacanthos*-invaded and uninvaded grasslands, with the top 3 contributing taxa and their contribution percentages at five Free State locations.

Location	Avg. dis. %	Taxon	Contribution %
Willows	73.1	*Pheidole* sp. 01	13,53
		Pheidole megacephala	11,86
		Monomorium sp. 01	4,11
700	74.28	*Monomorium* sp. 01	7,56
		Pheidole sp. 02	4,96
		Pheidole megacephala	4,94
Clarens 1	86.04	*Anoplolepis custodiens*	11,24
		Leptogenys cf *intermedia*	5,87
		Monomorium sp. 01	5,24
Clarens 2	85.72	*Tenebrio molitor*	10,63
		Anoplolepis custodiens	8,65
		Leptogenys cf intermedia	7,02
Kroonstad	61.3	*Tetramorium sericeiventre*	5,37
		Tetramorium sp. 01 (*setigerum* gp)	4,96
		Camponotus cintellus	4,91

In all the sampled locations, the uninvaded grasslands generally had more taxa, except for Clarens 1, although taxa differences were only significant at Willows (Table 2). Species diversity (Simpson's and Shannon's Indices) was higher at the uninvaded grasslands of Willows, Clarens 1 and Clarens 2, but these differences were not significant in any of the sampled locations. Species dominance was higher in the invaded grasslands of all the sampled locations; however, the differences were also insignificant (Table 2).

Table 2
Similarity percentage and diversity indices of arthropod communities in *G. triacanthos*-invaded and adjacent uninvaded sites across five grassland locations in the Free State province.

Location	Site	Species richness	Simpson index (1-D)	Shannon's Index (H)	Dominance
Willows	Uninvaded	21.25 ± 5.32[a]	0.25 ± 0.11[a]	0.68 ± 0.24[a]	0.76 ± 0.11[a]
	Invaded	12.25 ± 2.99[b]	0.14 ± 0.05[a]	0.37 ± 0.12[a]	0.86 ± 0.05[b]
R700	Uninvaded	23.75 ± 8.05[a]	0.74 ± 0.20[a]	2.03 ± 0.57[a]	0.21 ± 0.11[a]
	Invaded	17.75 ± 5.62[a]	0.83 ± 0.07[a]	2.28 ± 0.21[a]	0.25 ± 0.22[a]
Clarens 1	Uninvaded	20.25 ± 11.06[a]	0.86 ± 0.06[a]	2.37 ± 0.49[a]	0.14 ± 0.06[a]
	Invaded	24.75 ± 12.28[a]	0.68 ± 0.13[a]	1.69 ± 0.37[a]	0.32 ± 0.13[a]
Clarens 2	Uninvaded	24.5 ± 16.42[a]	0.76 ± 0.14[a]	2.06 ± 0.41[a]	0.22 ± 0.09[a]
	Invaded	11 ± 7.87[a]	0.75 ± 0.14[a]	1.76 ± 0.37[a]	0.25 ± 0.14[a]
Kroonstad	Uninvaded	28.5 ± 10.08[a]	0.76 ± 0.18[a]	2.06 ± 0.55[a]	0.19 ± 0.08[a]
	Invaded	27 ± 8.04[a]	0.80 ± 0.06[a]	2.16 ± 0.32[a]	0.20 ± 0.06[a]

Ants were the most abundant order throughout the seasons (Fig. 3). Their abundance was significantly affected by invasion and season across all sampled locations, excluding Willows, where both season and invasion had no significant effect. Ant abundance was generally higher in the uninvaded grasslands, especially in summer and autumn, except for Clarens 1 (Fig. 3c), where abundance was higher under *G. triacanthos*, but there were still more species in the uninvaded grassland (Appendix 1).

There were generally more beetle species in the uninvaded grasslands, with richness peaking in summer (Appendix 1). Abundance was significantly affected by season in all sampled locations, and it was generally higher in the uninvaded grasslands; However, the difference was only significant in Clarens 2 (Fig. 3d). Blattodea (cockroaches and termites) were more abundant under *G. triacanthos*; however, the difference was only significant in R700 and Kroonstad (Fig. 3b and e). Seasonal difference was only significant in R700 and Clarens 2 (Fig. 3b, d).

Grasshoppers were more speciose and abundant in the uninvaded grasslands, although the abundance differences between invaded and uninvaded grasslands were only significant in R700, Clarens 2 and Kroonstad (Appendix 1; Fig. 3b, d, e).

Discussion

The study investigated the diversity and assemblage composition of four insect orders in grassland stands invaded by *Gleditsia triacanthos* compared to uninvaded grasslands. Our findings show that insect communities significantly differ in composition and abundance between these grassland stands. Uninvaded grasslands had higher species richness and lower dominance, although the differences were insignificant. These findings align with previous studies showing that invasive alien plants can alter and reduce arthropod communities. For example, Rodríguez et al. (2020) found reduced insect abundance, including beetles and flies, in Iberian Peninsula coastal areas invaded by *Carpobrotus edulis* (L.) Brown (Aizoaceae). While Chikowore et al. (2021) demonstrated that *Robinia pseudoacacia* L. (Fabaceae) invasion in the Northern Slopes of the Maluti-Drakensberg Mountains, South Africa, significantly reduced arthropod diversity and abundance, particularly grasshoppers, beetles, and ants, due to altered habitat structure and microclimate.

Invasive alien plants often reduce habitat suitability by suppressing native plant communities and forming dense monocultures (Linders et al. 2019; Rai and Singh 2020). When a single plant species dominates, as seen in *G. triacanthos* invaded grasslands, habitat quality and quantity shift, leading to changes in diversity and community composition (Litt and Steidl 2010; Litt et al. 2014). Generally, uninvaded ecosystems support higher species diversity due to co-evolution between plants and arthropods (e.g. Burghardt et al. 2010). However, plant invasions drive physical and microclimatic changes that reshape these communities, causing bottom-up effects on higher trophic levels (Schrimel et al. 2016).

The invasion-driven shifts are evident in the dominance of certain insect groups and can displace less competitive taxa. For example, in all sampled locations, ants were the most dominant contributors to the observed species matrix, particularly those from the genera *Pheidole* and *Anoplolepis* (Table 1). *Pheidole* was a highly numerically dominant ant genus in the invaded sites of Willows and R700. The ant genus *Pheidole* is known to be hyperdiverse and widely distributed, with many unidentifiable morphospecies (Wilson 2003; Fischer et al. 2012). This genus has a wide range of feeding strategies and habitat requirements, but a common trait is their ability to form large colonies and monopolise food sources (Casadei Ferreira 2021). For example, a species in this genus, *P. megacephala*, thrives in open, disturbed environments where it can attain high densities and exclude other species (Wetterer 2012).

Similarly, *Anoplolepis custodiens*, which dominated the invaded sites in both Clarens and Kroonstad, is a hyperabundant, disturbance-tolerant species that prey on other invertebrates and displaces other ant species (Munyai et al. 2020), thus homogenising arthropod assemblages. Mauda et al. (2018) also found that *A. custodiens* responds to disturbance by becoming numerically dominant.

Conversely, an ant genus, *Monomorium* was more abundant in the uninvaded sites of R700 and Kroonstad (Appendix 1). The *Monomorium* genus is also highly speciose and lacks clear autapomorphies (Heterick 2006). Species in the ant genus *Monomorium* are often small, slow-moving, and unaggressive (Andersen et al. 1991). This could explain their greater presence in the uninvaded stands, where different species co-exist and competition is lower.

Invasive alien trees in grasslands, such as *G. triacanthos*, alter microclimates due to their tall canopies, which reduce light availability, limit moisture and modify ground temperatures (Kaizer-Bonk et al. 2016; Yapi et al. 2018; Chikowore et al. 2021; Gallé et al. 2023). These environmental shifts can directly affect insect assemblages, as these ectothermic organisms are susceptible to temperature fluctuations and habitat disturbances. Additionally, invasive alien plants can indirectly affect arthropod communities by reducing plant diversity, thus limiting resource availability and intensifying competition for resources (Linders et al. 2019).

Interestingly, our results reveal that some of the identified genera, such as those in ant genera, *Camponotus* and *Lepisiota* ants, *Tenebrio* (beetles) and cockroaches, were also abundant in the invaded sites (Appendix 1). This highlights how invasive alien plants can serve as a more suitable food source for certain species (Schlaepfer et al. 2005; Drossart et al. 2017). For instance, the sugar-rich pods of *G. triacanthos* likely attract species like ants and beetles and the omnivorous and opportunistic cockroaches, supporting their higher abundances in invaded sites. Some insect species can also shift their food source or oviposition host plants, favouring invasive plants over time (e.g., Keeler and Chew 2008; Drossart et al. 2017). The increased abundance of some species, coupled with the reduction or exclusion of others, likely contributes to the higher species dominance observed in the invaded sites (Table 1). The increase shows that *G. triacanthos* reshapes community dynamics by favouring generalist and opportunistic species over specialists that thrive in the more diverse uninvaded sites.

The increased abundance of some arthropods, such as cockroaches, termites and some ant species in *G. triacanthos* invaded grassland may also be due to the increased organic matter, as many of them are omnivores and detritivores (King 2016). Similar results were reported by Effah et al. (2020), who found that detritivorous oribatid mites and fungivorous beetles, such as the silken fungus beetles, were more abundant in sites invaded by *Cytisus* scoparius (L.) Link (Fabaceae) due to the increased decaying vegetation, which increases organic matter in the soil. Mahlobo et al. (2025) found that soils under *G. triacanthos* had higher nutrient pools, including organic carbon, nitrogen and phosphorus. Higher diversity and abundance were also observed in summer and autumn, and they decreased in winter (Fig. 3), indicating that ground temperature and nutrient availability, both influenced by *G. triacanthos*, may be shaping insect communities.

Conclusion

Our study shows that *Gleditsia triacanthos* invasion reshapes insect communities in grasslands by reducing species richness and abundance, although the reduction in richness and diversity was not

statistically significant. The results also highlight the site-specific impacts of *G. triacanthos* and how this invasive species can restructure insect assemblages through changes in both biotic and abiotic factors, with potential consequences for broader ecosystem processes.

Our findings also highlight the need for further research into the specific traits of the tree that are driving these changes and how other environmental factors may be contributing to shifts in insect community structure.

Declarations

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author Contribution

Author contributionsTM: Funding acquisition, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft. GM: Conceptualisation, Funding acquisition, Resources, Writing – review & editing. CM: Resources, Writing – review & editing. ND: Conceptualisation, Funding acquisition, Resources, Project administration, Methodology, Writing – review & editing.

Acknowledgement

AcknowledgementsThis study was funded by the National Research Foundation (NRF) under the Thuthuka funding instrument and the Centre for Biological Control (CBC). The landowners are thanked for granting consent to collect samples on their farms. We also sincerely thank Abusisiwe Ndaba for the assistance with ant identification.

Data Availability

Data is available from the main author upon reasonable request.

References

1. Alekseev V, Napreenko M, Napreenko-Dorokhova T (2024) Ecological Groups of Coleoptera (Insecta) as Indicators of Habitat Transformation on Drained and Rewetted Peatlands: A Baseline Study from a Carbon Supersite. Kaliningrad Russia Insects 15:356–383. https://doi.org/10.3390/insects15050356
2. Almeida FS, Elizalde L, Silva LMS, Queiroz JM (2019) The effects of two abundant ant species on soil nutrients and seedling recruitment in Brazilian Atlantic Forest. Rev Bras Entomol 63:296–301. https://doi.org/10.1016/j.rbe.2019.08.001

3. Andersen AN, Blum MS, Jones TH (1991) Venom alkaloids in *Monomorium rothsteini* Forel repel other ants: is this the secret to success by *Monomorium* in Australian ant communities? Oecologia 88:157–160. https://doi.org/10.1007/bf00320805
4. Salgado SE (2021) Evaluation of *Megabruchidius tonkineus* (Coleoptera: Chrysomelidae: Bruchinae), a candidate biological control agent for *Gleditsia triacanthos* L. (Fabaceae) in South Africa. MSc thesis, Rhodes University, South Africa
5. Belovsky GE, Slade JB (2018) Grasshoppers affect grassland ecosystem functioning: Spatial and temporal variation. Basic Appl Ecol 26:24–34. https://doi.org/10.1016/j.baae.2017.09.003
6. Blair RM (1990) *Gleditsia triacanthos* L., honeylocust. Silvics North Am 2:358–364
7. Burghardt KT, Tallamy DW, Philips C, Shropshire KJ (2010) Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. Ecosphere 1(5):1–22. https://doi.org/10.1890/es10-00032.1
8. Casadei Ferreira A (2021) Pheidole. In: Starr CK (ed) Encyclopaedia of Social Insects. Springer, Cham. https://doi.org/10.1007/978-3-030-28102-1_172
9. Chikowore G, Martin GD, Chidawanyika F (2021) An assessment of the invasive alien tree, *Robinia pseudoacacia* canopy traits and its effect on grassland microclimates and subsequent arthropod assemblages. J Insect Conser 25:429–439. https://doi.org/10.1007/s10841-021-00311-0
10. Drossart M, Michez D, Vanderplanck M (2017) Invasive plants as potential food resource for native pollinators: A case study with two invasive species and a generalist bumble bee. Sci Rep 7:16242. https://doi.org/10.1038/s41598-017-16054-5
11. Effah E, Barrett DP, Peterson PG, Potter MA, Holopainen JK, Clavijo McCormick A (2020) Effects of two invasive weeds on arthropod community structure on the Central Plateau of New Zealand. Plants 9(7):919. https://doi.org/10.3390/plants9070919
12. Enebe MC, Erasmus M (2024) Blatticomposting–a perspective on cockroach-mediated waste valorization to nutrient-rich organic fertilizer for enhancing soil health. Soil Adva 2:100012. https://doi.org/10.1016/j.soilad.2024.100012
13. Fernandez RD, Ceballos SJ, Malizia A, Aragón R (2017) *Gleditsia triacanthos* (Fabaceae) in Argentina: a review of its invasion. Aust J Bot 65:203–213. http://dx.doi.org/10.1071/BT16147
14. Fisher BL, Bolton B (2016) Ants of Africa and Madagascar: a guide to the genera. University of California Press, California, United States of America
15. Fischer G, Garcia FH, Peters MK (2012) Taxonomy of the ant genus *Pheidole* Westwood (Hymenoptera: Formicidae) in the Afrotropical zoogeographic region: definition of species groups and systematic revision of the *Pheidole pulchella* group. Zootaxa 3232:1–43. https://doi.org/10.11646/zootaxa.3232.1.1
16. Gallé R, Tölgyesi C, Szabó ÁR, Korányi D, Bátori Z, Hábenczyus A, Török E, Révész K, Torma A, Gallé-Szpisjak N, Lakatos T (2023) Plant invasion and fragmentation indirectly and contrastingly affect native plants and grassland arthropods. Sci Total Environ 903:166199. https://doi.org/10.1016/j.scitotenv.2023.166199

17. Garcia RA, Clusella-Trullas S (2017) Impacts of invasive plants on animal diversity in South Africa: A synthesis. Bothalia 47:1–12. https://doi.org/10.4102/abc.v47i2.2166
18. GBIF.org (2024) GBIF Occurrence. https://doi.org/10.15468/dl.588y7n
19. Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. J insect conserv 17:831–850. https://doi.org/10.1007/s10841-013-9565-9
20. Hammer Ø, Harper DA (2001) Past: paleontological statistics software package for education and data analysis. Palaeontol electronica 4:1
21. Henderson L, Wilson JR (2017) Changes in the composition and distribution of alien plants in South Africa: An update from the Southern African Plant Invaders Atlas. Bothalia-Afr Biodivers Conserv. 47(2):1–26. https://doi.org/10.4102/abc.v47i2.2172
22. Heterick BE (2006) A revision of the Malagasy ants belonging to the genus *Monomorium* Mayr, 1855 (Hymenoptera: Formicidae). Proc Cal Acad Sci 59:719–722. https://doi.org/10.1071/it00003
23. Jouquet P, Traoré S, Choosai C, Hartmann C, Bignell D (2011) Influence of termites on ecosystem functioning. Ecosystem services provided by termites. Eur J Soil Biol 47(4):215–222. https://doi.org/10.1016/j.ejsobi.2011.05.005
24. Kaizer-Bonk J, Szpiłyk D, Woyciechowski M (2016) Invasive goldenrods affect abundance and diversity of grassland ant communities (Hymenoptera: Formicidae). J Insect Conserv 20:99–105. https://doi.org/10.1007/s10841-016-9843-4
25. Keeler MS, Chew FS (2008) Escaping an evolutionary trap: preference and performance of a native insect on an exotic invasive host. Oecologia 156:559–568. https://doi.org/10.1007/s00442-008-1005-2
26. King JR (2016) Where do eusocial insects fit into soil food webs? Soil Biol Biochem 102:55–62. https://doi.org/10.1016/j.soilbio.2016.07.019
27. Kwon TS, Park YK, Jung JK, Lee YG, Park CW, Park YS (2022) Effects of preservatives in pitfall traps for collecting arthropods: A comparison of ethylene glycol and five alternative preservatives. J Asia-Pac Biodivers 15:541–546. https://doi.org/10.1016/j.japb.2022.07.001
28. Laws AN, Prather CM, Branson DH, Pennings SC (2018) Effects of grasshoppers on prairies: Herbivore composition matters more than richness in three grassland ecosystems. J Anim Ecol 87:1727–1737. https://doi.org/10.1111/1365-2656.12897
29. Linders TE, Schaffner U, Eschen R, Abebe A, Choge SK, Nigatu L, Mbaabu PR, Shiferaw H, Allan E (2019) Direct and indirect effects of invasive species: Biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning. J Ecol 20:2660–2672. https://doi.org/10.1111/1365-2745.13268
30. Litt AR, Cord EE, Fulbright TE, Schuster GL (2014) Effects of invasive plants on arthropods. Conserv Biol 28:1532–1549. https://doi.org/10.1111/cobi.12350
31. Litt AR, Steidl RJ (2010) Insect assemblages change along a gradient of invasion by a nonnative grass. Biol Invasions 12:3449–3463. https://doi.org/10.1007/s10530-010-9743-6

32. Lusizi Z, Motsi H, Nyambo P, Elephant D (2024) Black (*Acacia mearnsii*) and silver wattle (*Acacia dealbata*) invasive tree species impact on soil physicochemical properties in South Africa: A systematic literature review. Heliyon 10(2):e24102. https://doi.org/10.1016/j.heliyon.2024.e24102
33. Mahlobo T, Zondo S, Martin GD, Munyai CT, Dube N (2025) Impacts of *Gleditsia triacanthos* L. (Fabaceae) on soil characteristics: insights from the Free State Highveld grasslands of South Africa. Biol Invasions 27:128. https://doi.org/10.1007/s10530-025-03616-2
34. Maldonado MB, Aranibar JN, Serrano AM, Chacoff NP, Vázquez DP (2019) Dung beetles and nutrient cycling in a dryland environment. CATENA 179:66–73. https://doi.org/10.1016/j.catena.2019.03.035
35. Malongweni SO, Mrubata K, van Tol J, Abd Elbasit MA, Harebottle DM (2025) Consequences of Invasive *Prosopis* (Mesquite) on Vegetation, Soil Health, Biodiversity, and Compliance of Management Practices in South African Rangelands: A Review. Grasses 4(1):2. https://doi.org/10.3390/grasses4010002
36. Martin GD (2021) Prospects for the biological control of Northern Temperate Weeds in South Africa. Afri Entomol 29:791–808. https://doi.org/10.4001/003.029.0791
37. Mauda EV, Joseph GS, Seymour CL, Munyai TC, Foord SH (2018) Changes in land use alter ant diversity, assemblage composition and dominant functional groups in African savannas. Biodivers Conserv 27:947–965. https://doi.org/10.1007/s10531-017-1474-x
38. Montesinos D, Castro S, Rodríguez-Echeverría S (2016) Two invasive acacia species secure generalist pollinators in invaded communities. Acta Oecol 74:46–55. http://dx.doi.org/10.1016/j.actao.2016.06.002
39. Munyai TC, Foord S, Slotow R, Mkhize N (2020) A Pugnacious ant (*Anoplolepis custodiens*) confounds ant assemblage responses to bush encroachment. Authorea Preprints. https://doi.org/10.22541/au.160630390.02526653/v1
40. Picker M, Griffiths C, Weaving A (2019) Field guide to insects of South Africa. 3rd Edition. Struik Nature. Century City, South Africa
41. Prinsloo H, Reilly B, Myburgh W (2021) Identifying potential protected areas in the Grassland Biome of South Africa. S Afr J Sci 117:1–6. https://doi.org/10.17159/sajs.2021/7507
42. Rai PK, Singh JS (2020) Invasive alien plant species: Their impact on environment, ecosystem services and human health. Ecol Indic 111:106020. https://doi.org/10.1016/j.ecolind.2019.106020https://doi.org/10.1016/j.ecolind.2019.106020
43. Rodríguez J, Cordero-Rivera A, González L (2020) Characterizing arthropod communities and trophic diversity in areas invaded by Australian acacias. Arthropod-Plant Interact 14:531–545. https://doi.org/10.1007/s11829-020-09758-5
44. Rodríguez J, Thompson V, Rubido-Bará M, Cordero-Rivera A, González L (2019) Herbivore accumulation on invasive alien plants increases the distribution range of generalist herbivorous insects and supports proliferation of non-native insect pests. Biol Invasions 21(5):1511–1527. https://doi.org/10.1007/s10530-019-01913-1

45. Schlaepfer MA, Sherman PW, Blossey B, Runge MC (2005) Introduced species as evolutionary traps. Ecol Lett 8(3):241–246
46. Schirmel J, Bundschuh M, Entling MH, Kowarik I, Buchholz S (2016) Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: a global assessment. Glob Change Biol 22:594–603. https://doi.org/10.1111/gcb.13093
47. Solascasas P, Azcárate FM, Hevia V (2022) Edaphic arthropods as indicators of the ecological condition of temperate grassland ecosystems: A systematic review. Ecol Indic 142:109277. https://doi.org/10.1016/j.ecolind.2022.109277
48. van Wilgen BW, Measey J, Richardson DM, Wilson JR, Zengeya TA (2020) Biological Invasions in South Africa: An Overview. In: van Wilgen B, Measley J, Richardson DM, Wilson R, Zengeya TA (eds) Biological Invasions in South Africa. Springer Nature, Berlin, Germany, pp 3–31. https://doi.org/10.1007/978-3-030-32394-3_1
49. Vilches C, Torremorell AM, Rodriguez Castro MC, Giorgi A (2020) Effects of the invasion of honey locust (*Gleditsia triacanthos* L.) on macrophytes and algae of Pampean streams (Argentina). Wetl 40:321–331. https://doi.org/10.1007/s13157-019-01179-2
50. Wetterer JK (2012) Worldwide spread of the African big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). Myrmecol News 17: 51–62. https://doi.org/10.2984/1534-6188(2007)61[437:baiopi]2.0.co;2
51. Wilson EO (2003) *Pheidole* in the New World: a dominant, hyperdiverse ant genus, vol 1. Harvard University Press, Cambridge, USA
52. Yapi TS, O'Farrell PJ, Dziba LE, Esler KJ (2018) Alien tree invasion into a South African montane grassland ecosystem: impact of *Acacia* species on rangeland condition and livestock carrying capacity. Int J Biodivers Sci Ecosyst Serv Manag 14:105–116. https://doi.org/10.1080/21513732.2018.1450291

Figures

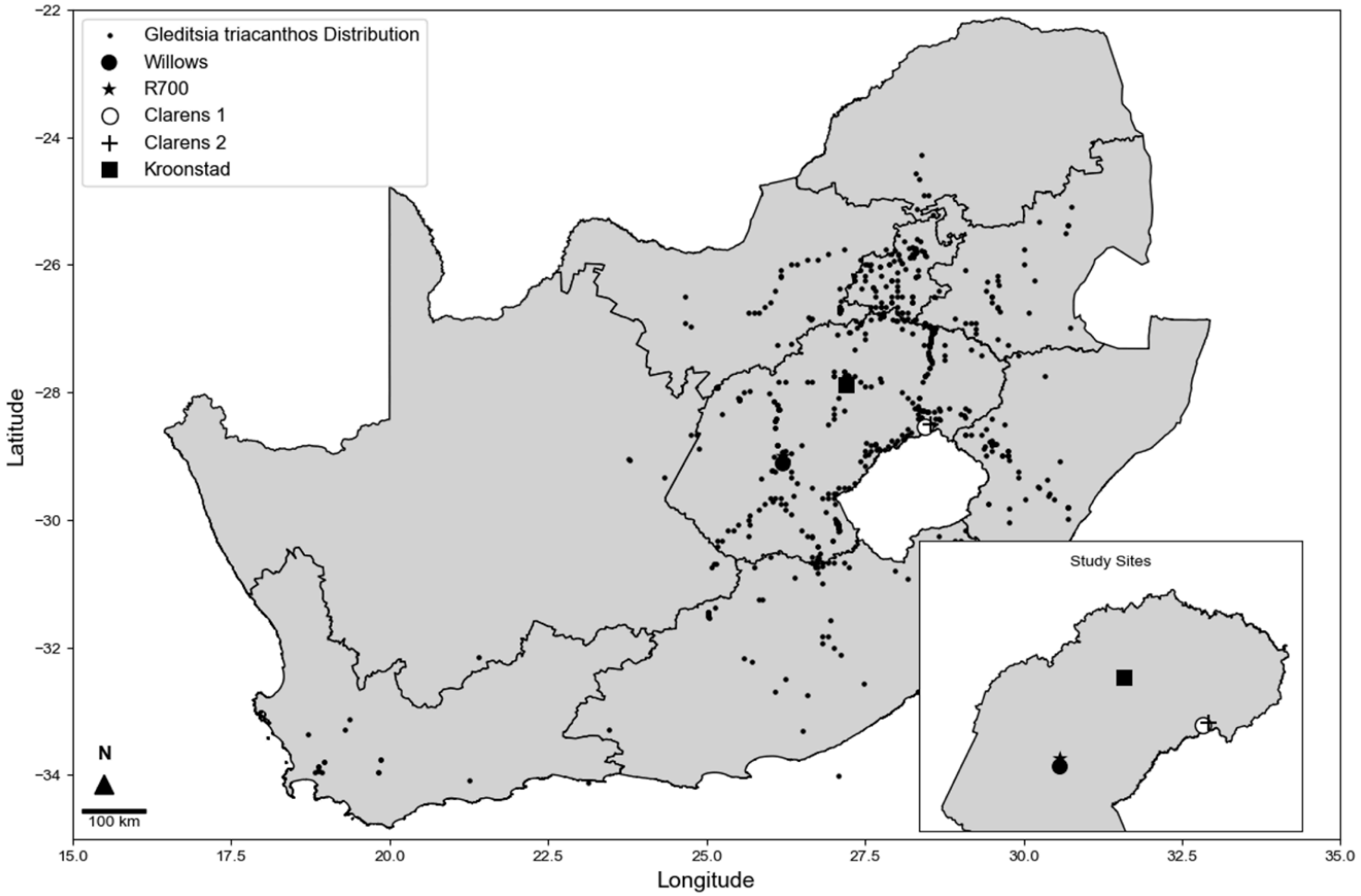

Figure 1

Distribution of *Gleditsia triacanthos* in South Africa and study sites in the Free State Province. Distribution data was adapted from the Southern African Plant Invaders Atlas database (SAPIA), INaturalist (2019), Global Biodiversity Information Facility (GBIF, 2024) and road surveys by Salgado (2021)

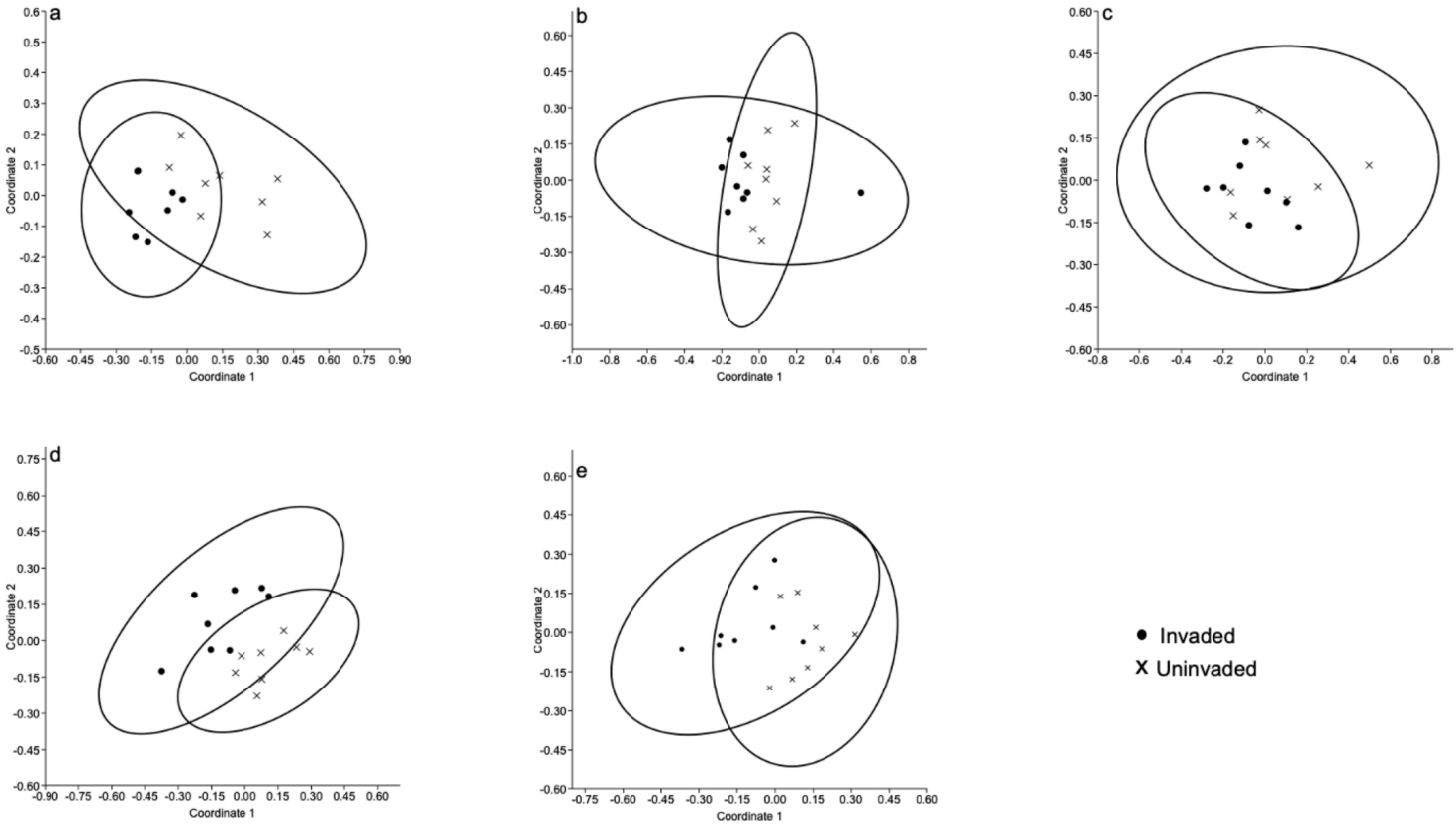

Figure 2

Non-metric multidimensional scaling (NMDS) ordination of arthropod communities in *G. triacanthos*-invaded and adjacent uninvaded sites across five grassland locations: (a) Willows, (b) R700, (c) Clarens 1, (d) Clarens 2, and (e) Kroonstad

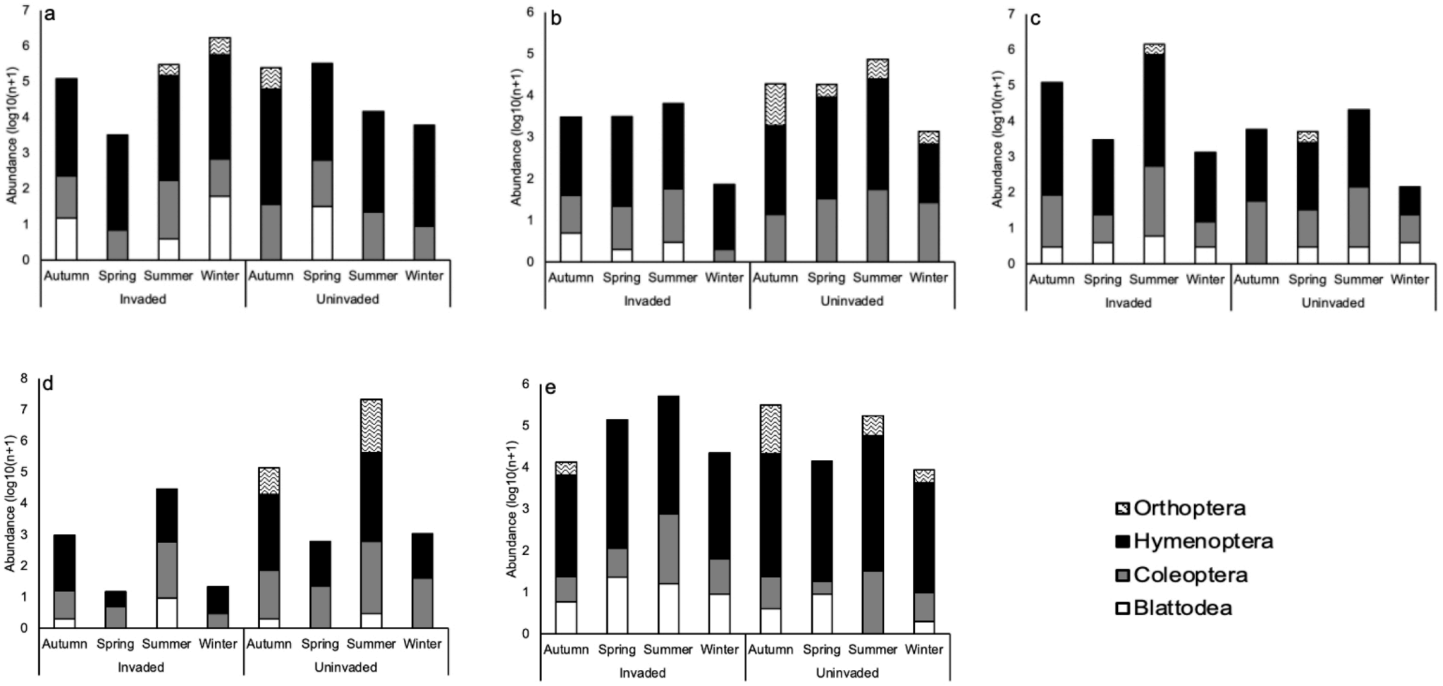

Figure 3

Arthropod species abundances in *G. triacanthos*-invaded and adjacent uninvaded sites across five grassland locations and seasons: (a) Willows, (b) R700, (c) Clarens 1, (d) Clarens 2, and (e) Kroonstad

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- MahloboetalAppendix1.pdf