

Post-dispersal seed removal in an agricultural landscape of semi-arid West Africa

Paula Antwiwaah N. Boadi

University for Development Studies

Jerry A. Nboyine

Council for Scientific and Industrial Research

Francis Kusi

Council for Scientific and Industrial Research

Ibrahim Yussif Jnr

Tamale Technical University

Eric Adjei Lawer (✉ ladjei@uds.edu.gh)

University for Development Studies

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Abstract

Post-dispersal seed removal is crucial for maintaining plant diversity by influencing secondary dispersal, recruitment, and mortality of seeds. In this study, we examined the effect of three habitat types (conventional farmland, agroforestry parkland, and woodland) and two seed species (*Leucaena leucocephala* and *Faidherbia albida*) on post-dispersal seed removal by invertebrates and vertebrates in an agricultural landscape using selective exclosure treatments. The exclosure treatments, closed and open, were designed to respectively impose restrictions that allow only invertebrates as well as both invertebrates and vertebrates access to seeds. The results showed that habitat type ($\chi^2=65.06$, $p = <0.0001$) and seed species ($\chi^2=6.207$, $p = 0.013$) influenced the rate of seed removal: i.e., the woodland habitat and *F. albida* seeds recorded the highest removal rates while the parkland habitat recorded the least. However, while not always statistically significant for most habitat pairwise comparisons for the different seed species investigated, our findings suggest that invertebrates likely dominated seed removal events compared to vertebrates. The diversity of fauna often associated with natural or woodland habitats coupled with their differential seed selection habits may have accounted for the observed findings. We further suspect that the presence of bushes and fallow lands near conventional farmlands resulted in its high seed removal rate compared to the parkland habitat. Thus, post-dispersal seed removal benefits from fauna diversity in bushes or fallows near conventional farmlands. Overall, our study has demonstrated that woodland and agricultural habitats can potentially contribute to maintaining plant population dynamics through predation and dispersal events.

1. Introduction

Post-dispersal seed removal is a type of plant-animal interaction which leads to secondary dispersal or predation of seeds that have been initially moved away from the parent plant (Herrera and Pellmyr 2002; Vander Wall et al. 2005). Predation leads to seed mortality while secondary dispersal results in the movement of seeds to new sites that may favor germination. This reduces the risk of local plant extinction as it decreases the competition for sunlight and minerals among plants that would have otherwise been in the same area. Thus, seed removal by animals can influence plant population dynamics and community structure by affecting seed survival and seedling recruitment in varying landscapes (Arnan et al. 2012).

Seed dispersal is dependent on the structure of the landscape and whether invertebrates or vertebrates are dispersing it. Studies have shown that the most pervasive post-dispersal seed removers are birds, rodents, and insects (Li Vigni and Melati 1999; Hulme 2002). Hence, plants that depend on animals for dispersal are susceptible to dispersal failure when seed dispersers become locally extinct or rare. This can seriously compromise the proper functioning of ecosystems and the provision of valuable ecosystem services such as seed dispersal and nutrient recycling in degraded environments (Pérez-Méndez et al. 2016; Gardner et al. 2019; Fedriani et al. 2020).

In recent years, conventional agriculture (i.e., farming) has expanded rapidly at the expense of the natural environment and other types of sustainable farming including agroforestry parkland (i.e., hereafter, parkland) systems in the West African region (Herrmann et al. 2020). Conventional farming systems rely on the intensive use of agrochemicals to maximize production which is in contrast to parkland systems where multipurpose woody perennials are intentionally retained alongside crops in a spatially scattered layout to ensure ecological sustainability (Pullan 1974; Nair 1985). Therefore, an increase in conventional farming can lead to the loss of natural and parkland habitats that have been shown to support both plant and animal diversity (McNeely and Schroth 2006; Scales and Marsden 2008; Fifanou et al. 2011).

The widespread decimation of vertebrate and invertebrate populations through habitat change or loss is expected to have devastating long-term consequences for maintaining biodiversity, particularly plant species through dispersal events (Lewis and Gripenberg 2008; de Paula Mateus et al. 2018). Because natural and parkland habitats can support a diverse group of vertebrates and invertebrates (McNeely and Schroth 2006; Scales and Marsden 2008), we assume that seed removal will be higher in these habitats compared to conventional farmland habitats. Nonetheless, little attention has been given to testing this assumption compared to seed germination and seed dormancy studies particularly in West Africa (Danthu et al. 2003; Koutouan-Kontchoi et al. 2020). For example, in Ghana, there is very limited research on seed predation and secondary dispersal in the northern savanna ecological zone compared to the few conducted in the forest zone of southern Ghana (Lieberman et al. 1979; Kankam and Oduro 2009; Abedi-Lartey et al. 2016). Therefore, the goal of this research is to investigate the role of invertebrates and vertebrates in post-dispersal seed removal in a semi-arid agricultural- landscape of northern Ghana (i.e., conventional farmland vs. parkland vs. woodland). An understanding of the dynamics of seed removal at this local scale will contribute to enhancing conservation efforts in the northern savanna ecological zone.

2. Methodology

2.1 Study area

The study was conducted in Nyankpala in the Tolon District of the Northern Region of Ghana. The area falls within the northern savanna ecological zone and has a unimodal rainfall pattern which occurs between April and October annually (GSS 2014).

Our seed removal experiment was performed in three different habitat types separated by a minimum distance of approximately 700 m: i.e., conventional farmland, parkland and woodland (Table 1). Ideally, conventional farmlands should contrast parklands as the latter seeks to promote ecological balance and the conservation of biodiversity by avoiding or limiting the use of agrochemicals as well as intensive tillage among other practices (Boffa 1999; Pantera et al. 2021; Sumberg and Giller 2022). However, in the study area, agrochemicals and other resources are usually applied similarly in both agriculture systems with the only notable difference being the presence or absence of woody plants. Even the abundance of woody plants in parklands are rapidly declining in the area due to unsustainable practices: e.g., intensive farming and fuelwood harvesting (Poudyal 2011). Studied cultivated lands consisted of smallholder

farms that are owned by local community members while the woodland habitat, which is a secondary woodland, is owned and managed by the Savanna Agricultural Research Institute, Nyankpala.

Table 1

Description of study habitats included in the investigation. Estimates of total woody plant components are based on three 25 m × 25 m quadrats established in each habitat type.

Habitat	Description	Richness	Abundance
Conventional farmland	Crop production on lands devoid of woody plants	0	0
Agroforestry parkland	Crop production under scattered woody plants	2	6
Woodland	An area of land dominated by woody plants with few grass or herb species	5	109

In this study, tillage, planting, and application of agrochemicals (i.e., herbicides) on cultivated lands occurred earlier on the parkland compared to the conventional farmland at the time of field investigations (at least a weeks' difference). Crops such as cowpea (*Vigna unguiculata* L.), maize (*Zea mays* L.), and pepper (*Capsicum* spp.) were commonly cultivated on the surveyed conventional farmland and parkland habitats. Woody plant abundance and richness was highest in the woodland habitat (i.e., *Combretum* sp., *Detarium* sp., *Lannea* sp., *Terminalia* sp., *Vitellaria paradoxa*) followed by the parkland habitat (i.e., *Mangifera indica*, *V. paradoxa*) (Table 1). Although woody plants were absent from the conventional farmland and its immediate periphery, it was surrounded by bushes and fallow lands.

2.2 Study species

The seeds of *Faidherbia albida* and *Leucaena leucocephala* species were used in this study because they are commonly associated with agroforestry practices in the northern savanna ecological zone of Ghana. *F. albida* seeds are approximately 6–8 mm long and 4–5 mm wide while *L. leucocephala* seeds are approximately 6–10 mm long and 4–6 mm wide (Snieszko and Stewart 1989; Lim 2012). Both seed species can be dispersed by insects, rodents, and wind due to their relatively small size (Yirgu and Tsega 2015; Sharma et al. 2022). Matured non-burst seeds of these species were collected from the study area in January 2022 and stored to prevent insect damage before field experiments.

2.3 Post-dispersal seed removal experiment

We used an experimental setup designed to either exclude or allow access to seeds by different taxa in the various habitat sites. To allow access to seeds by only invertebrates, we used a cylindrical metallic cage with a mesh size of 1.2 cm × 1.2 cm and referred to it as 'closed treatment' (cage dimension: height = 15 cm and diameter = 21 cm). However, we did not use an exclosure cage for the 'open treatment' because we wanted all seeds to be available to all seed predators (i.e., invertebrates and vertebrates, specifically rodents and birds).

In each habitat type, we established three transects that were separated by a minimum distance of 100 m for the deployment of seed removal treatments. Each transect had five seed stations that were 10 to 20 m apart with each station consisting of a pair of open and closed treatments that were between 1 and 3 m apart. For each treatment, ten seeds of each seed species were placed on a plastic plate for the removal experiment. All seed stations were monitored daily for seed removal data in the rainy season (period of the experiment: June 09–23, 2022). The experiment was repeated after days of rainfall because rain could lead to false seed removal, which is not attributable to fauna. Hence, complete seed removal data for the latter period of this investigation (June 16–23) was extracted and used for all analyses due to the absence of rainfall.

2.4 Statistical analysis

All statistical analyses were conducted in R programming software (R Core Team 2022). A generalized linear mixed effects model (GLMM) with a beta error distribution was used to test the effect of the following predictor variables on post-dispersal seed removal rate: habitat type, seed species and exclosure treatment. The dependent variable, seed removal rate (R), was defined as the proportion of seeds removed per species after 48 h using the equation $R = N_{removed} / N_{offered}$ (Meyer et al. 2017): i.e., where $N_{removed}$ is the number of seeds removed after 48 h and $N_{offered}$ represents the total number of seeds per species placed at each seed station, which was 10. Additionally, we applied the transformation $(R * (n - 1) + 0.5) / n$ where n is the sample size because R assumed extreme values of 0 and 1 (Smithson and Verkuilen 2006; Cribari-Neto and Zeileis 2010). Transects were included as a random effect to eliminate the effect of spatial pseudo-replication in the model. Due to the significance of interaction terms (i.e., habitat $\times$ Seed species) in the main model, we fitted separate models for each species to determine the effect of habitat and exclosure on post-dispersal seed removal (e.g., Rocha-Ortega et al., 2017). All GLMMs were performed using the package glmmTMB (Brooks et al. 2017).

3. Results

Observations from the post-dispersal seed removal experiment showed that seed removal at seed stations after seven days was highest in the woodland habitat while the lowest was recorded in the parkland habitat. Seed removal within the woodland habitat terminated earlier than the conventional farmland and parkland habitat, with the latter two progressing beyond the sixth day of experimental monitoring (Fig. 1). Majority of seed removal events for both species occurred within 72 h of the experiment in the various habitats (Fig. 1). In both conventional farmland and parkland habitats, approximately 2 times more seeds of *F. albida* were removed compared to *L. leucocephala* after 48 h. In the woodland habitat, an equivalent proportion of seeds were removed for both species (Table 2). Overall, the presence of woody plants in habitats appeared to be moderately correlated with seed removal (Kendall's correlation: tau = 0.437, $p = < 0.0001$).

Table 2
Summary statistics for the post-dispersal seed removal experiment after 48 h (Med. refers to median value)

Habitat	<i>Faidherbia albida</i>			<i>Leucaena leucocephala</i>		
	No. removed (%)	Med.	Mean $\pm$ SD	No. removed (%)	Med.	Mean $\pm$ SD
Farmland	95 (31.7)	3	3.17 $\pm$ 1.42	36 (12)	1	1.2 $\pm$ 0.9
Parkland	47 (15.7)	2	1.6 $\pm$ 1.1	19 (6.3)	0.5	0.6 $\pm$ 0.7
Woodland	176 (58.7)	6	5.9 $\pm$ 1.5	186 (62)	6	6.2 $\pm$ 1.7

The main model showed that habitat type and seed species have significant effects on post-dispersal seed removal rate while the enclosure predictor was not significant. All interactions were significant except for the one between habitat and enclosure as well as the one between habitat, seed species and enclosure (Table 3). Results of separate GLMMs for each species are presented in Fig. 2. The effect of invertebrates on the seed removal rate of both seed species was significantly higher in woodland than in conventional farmland and parkland habitats. A similar pattern was observed for 'all predators' in the area except for the pairwise comparison between conventional farmland and parkland habitats ($p = 0.181$). The statistical significance between the 'all predator' and invertebrate groups in the conventional farmland indicates that rodents and birds were comparatively more important than invertebrates in influencing seed removal rate in the habitat. However, in the woodland habitat, invertebrates tend to play a key role in seed removal events given the marginal significance of this effect ($p = 0.045$). Nevertheless, the overall pattern of statistical non-significance in seed removal rate between the invertebrate and 'all predator' groups in the habitats indicates that the invertebrate group was relatively more important for post-dispersal seed removal compared to vertebrates such as rodents and birds (Fig. 2).

Table 3
Effects of habitat, seed species and enclosure on post-dispersal seed removal after 48 h. Results are obtained from a GLMM test with transect as a random effect. Significant p-values are in italics.

Predictor	df	Chisq.	p-value
Habitat	2	65.0601	<i>< 0.0001</i>
Seed	1	6.2065	<i>0.0127</i>
Exclosure	1	8.2699	<i>0.004</i>
Habitat×Seed	2	17.8018	<i>0.0001</i>
Habitat×Exclosure	2	3.6241	0.1633
Seed×Exclosure	1	7.5365	<i>0.0060</i>
Habitat×Seed×Exclosure	2	3.4275	0.1802

4. Discussion

This study sheds light on the influence of agroecosystems and predators on post-dispersal seed removal patterns in a semi-arid savanna landscape. Our findings confirm that the conversion of natural habitats such as woodlands to agriculture negatively affects post-dispersal services (Escobar et al. 2020; Rey et al. 2021). In this study, the seed removal rate was significantly higher in the woodland habitat than in the agricultural habitats. Low disturbance in the woodland habitat implies that it can support a diverse community of seed predators such as insects, birds and rodents (Fenton et al. 1998; Thiollay 2006; Nyirenda et al. 2020), which may have accounted for the high removal patterns observed in the study.

Contrary to our expectation, we found that the seed removal rate was significantly lower in parklands compared to conventional farmlands. Differences in cropping and insecticide application times between the investigated conventional farmland and parkland habitats may have accounted for the observed statistical difference. In our study, the parkland habitat was tilled, cropped and received pesticide treatment earlier than the conventional farmland habitat: i.e., pesticides were not applied on conventional farmlands at the onset of our experiment. Thus, we suspect that the lower rate of seed removal in parklands may be due to the loss of predators and their habitats caused by tillage and pesticide application (Sarabi 2019; Sánchez-Bayo 2021). In addition, the conventional farmland unlike the parkland was near bushes and fallow lands, thus influencing their ability to recover after tillage and pesticide use (Holland and Luff 2000; Jacobsen et al. 2022). It was therefore likely that seed predators moved from the surrounding vegetation into the conventional farmland to predate on seeds thereby accounting for the higher removal rate compared to the parkland habitat. This could have additionally contributed to the moderate correlation observed between the abundance of woody plants and the number of seeds removed. Nevertheless, further data would be needed to confirm these plausible explanations.

We found seed removal by vertebrates (i.e., rodents and birds) to be comparatively more frequent than invertebrates in conventional farmlands while the converse was true for woodlands. Other studies have confirmed that vertebrates dominate seed removal in agroecosystems (Cardina et al. 1996; Tschumi et al. 2018). Nonetheless, our findings while not significant for most comparisons in habitats across each seed species suggest that invertebrates generally dominated seed removal patterns. In terrestrial environments, invertebrates are among the most diverse faunal groups, which may explain the substantial role they offer in semi-arid and arid (savanna) ecosystems particularly in relation to pre- and post-dispersal seed predation (Ferrante et al. 2021).

Additionally, the use of only small-seeded species in our experiment most likely led to the frequent removal of seeds by invertebrates because they are relatively easier to carry compared to large-seeded species (Pirk and de Casenave 2010). Nevertheless, the difference in seed species removed may be attributed to differential seed selection by invertebrates and vertebrates driven by seed quality traits such as chemical or nutritional (e.g., energy content) as well as structural (e.g., seed coat) properties (Kerley and Erasmus 1991; Foffová et al. 2020; Moore et al. 2022).

5. Conclusion

Our study has demonstrated that parkland, conventional farmland, and woodland habitats contribute to ecosystem services and functions. Particularly, the study revealed that post-dispersal seed removal benefited from conventional farming with adjacent fallow land practices than intensively cropped parklands. Invertebrates and vertebrates contribute to seed removal, which is likely mediated by the differential seed preferences of predators. Nevertheless, invertebrates were observed to be more frequently associated with seed removal in this study. The positive effect of the woodland habitat on post-dispersal seed removal was largely mediated by faunal diversity which is tightly linked to floral diversity and the absence of agronomic practices (i.e., tillage and agrochemicals). Overall, our findings suggest that woodland and agricultural habitats can potentially contribute to maintaining plant population dynamics through predation and dispersal events. However, the agroforestry parkland system as is currently practiced in the area, is likely to negatively impact biodiversity including post-dispersal seed removers due to farmer practices that are incompatible with sustainable farming.

Declarations

All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors and are aware that with minor exceptions, no changes can be made to authorship once the paper is submitted.

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Author Contributions

PANB: Investigation, Original Draft Preparation; **JAN:** Review and Editing; **FK:** Review and Editing; **IYJ:** Review and Editing; **EAL:** Conceptualization, Methodology, Formal Analysis, Original Draft Preparation. All authors reviewed and approved the final version of the manuscript.

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Data availability

Data used in this study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Ethical approval

Not applicable

Conflict of interest

The authors declares no competing interest.

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Figures

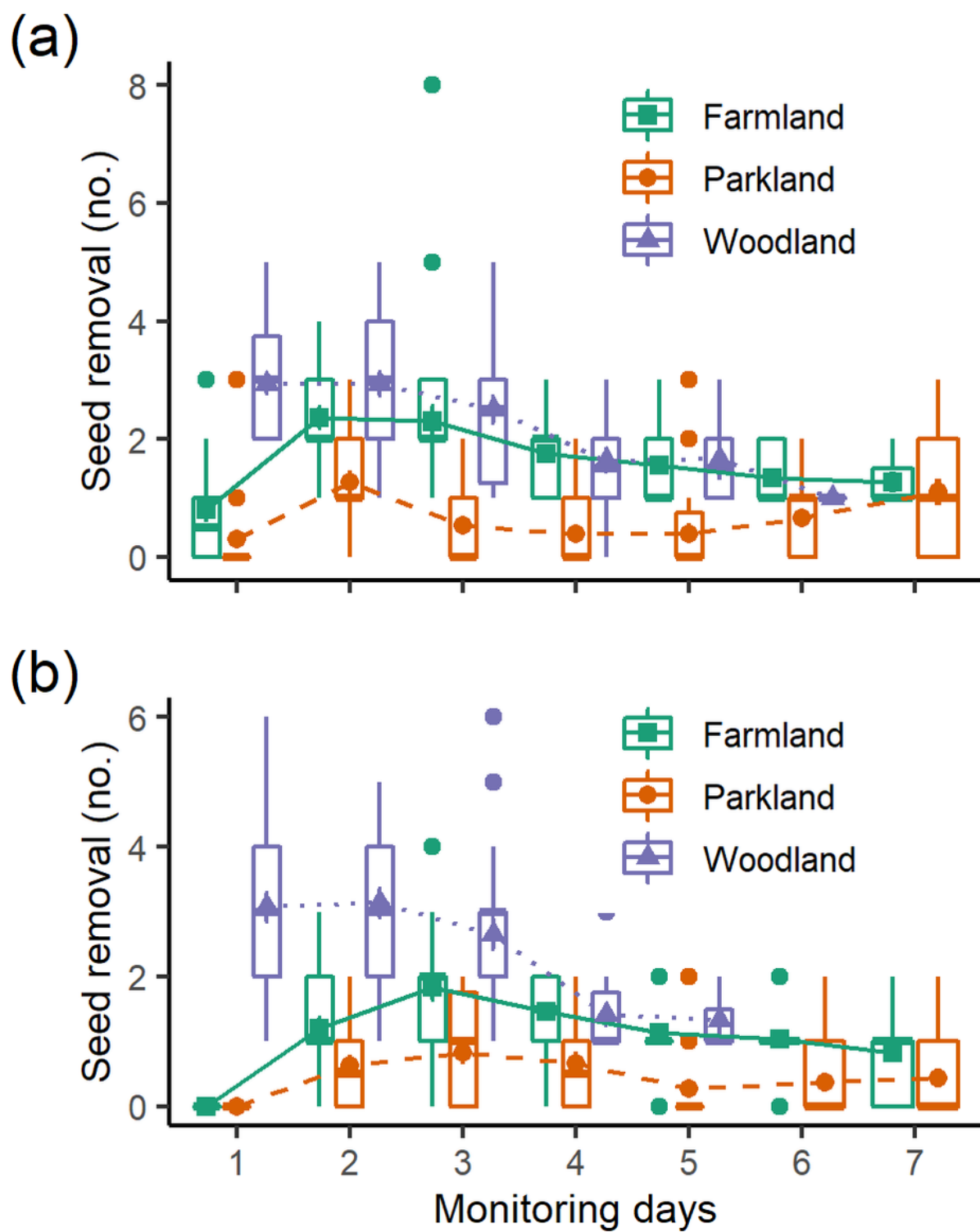


Figure 1

Number of seeds removed daily in the different habitats: a) *F. albida* and b) *L. leucocephala*

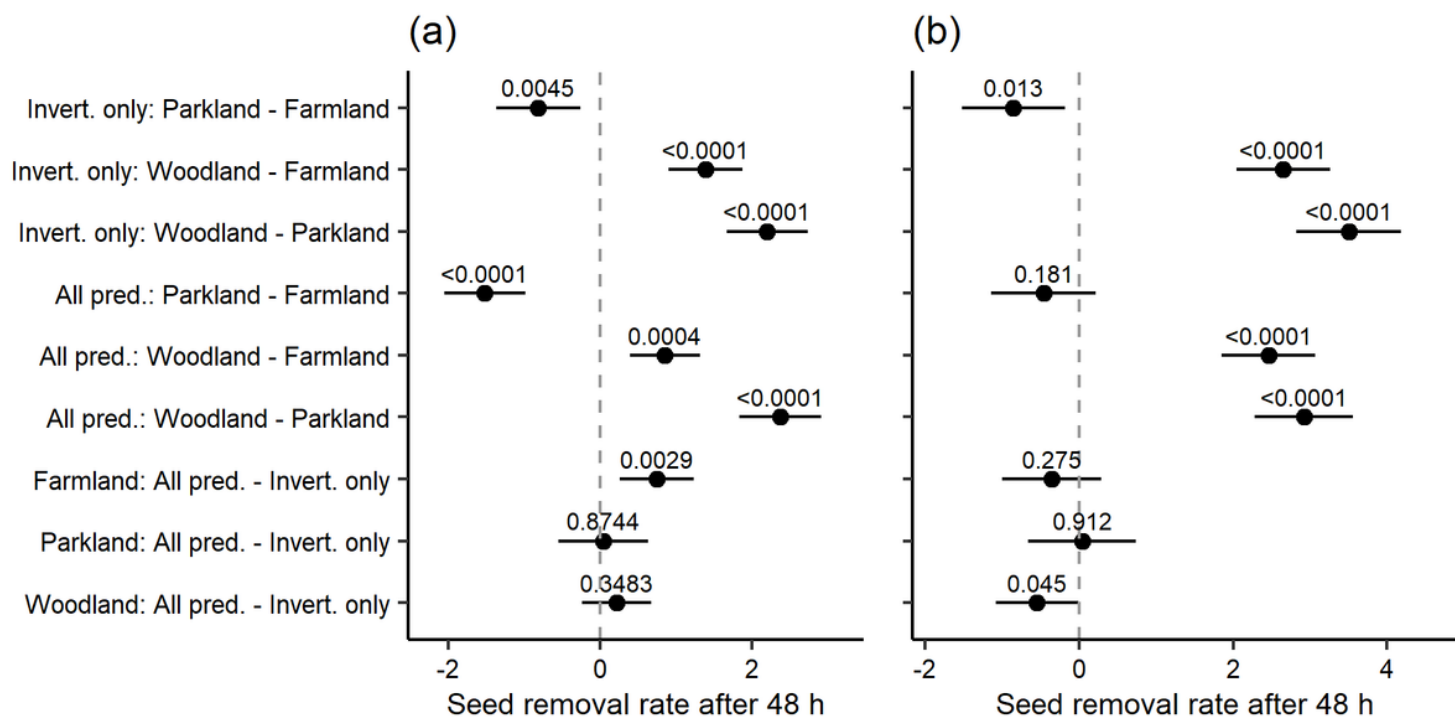


Figure 2

Effects of habitat and enclosure treatment on seed removal rate of a) *F. albida* and b) *L. leucocephala*. Estimates and 95% confidence intervals with associated p-values are derived from post-hoc simple main effect comparisons of GLMMs with transect set as a random effect. Where, Invert. = Invertebrates; All pred. = All predators (i.e., invertebrates and vertebrates).