

Influence of Connectivity on Dung Beetle Communities

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Abstract

Habitat fragmentation threatens biodiversity across the globe as habitat loss, isolation, and edge effects become increasingly prevalent. Corridors have become an important tool in order to combat the negative effects of fragmentation, however they are difficult to study in natural systems without incurring confounding effects. To observe changes in insect community composition as an effect of landscape features we sampled dung beetles in a landscape scale experiment. We did not see a difference in species richness or diversity, but dung beetle abundances were higher in continuous forest habitat and open habitat patches connected by a corridors than in isolated patches.

TO DO LIST

Next assignment:

1) Are any of the Dung Beetles we collected considered “open habitat” specialists? (might want to look at the work on pastures in the southeast)

- cvig - open sand chaparral, open grassland preference nealis 1977
- mbis - open sand chapparal preference nealis 1977
- open - slight preference towards open chap and shaded chap, little open grassland nealis 1977
- pign - sharing forest habitat but need more info conover 2019
- pvin - open habitat but share forest with pign conover 2019
- alec - forest preference conover 2019

2) Is there anything about these species that might be interesting in the context of corridors? Are any species known to be good fliers/movers? Specialists on deer dung? navigate by starlight?

- Ospina 2018: wing shape py habitat preference and differences in wing shape determined by species groupings. Beetles with wider wings showed more preference towards open habitat, contrary to what is already known in literature on other taxa (butterflies). Large body beetles tending towards lower energy flight strategies. maybe justification for corridor preference?
 - stanbrook and king 2022: tunnelers preferring open habitat and tunnelers also contributing more towards dung removal.
 - Conover 2019: dung source being less of an issue than habitat type but some species were more responsive to specific bait types so future studies should use a mix of multiple bait types

- Gimenez Gomez et al 2021 -> similar outcome some beetles were extra sensitive to specific baits so a mix of baits should be used. However this study was done in a more tropical ecosystem so its hard to say if the same would apply to our more temperate system so more work is needed in this specific avenue.

3) Did you get any species not captured in other long-leaf/SE USA forest sites?

4) What are hill numbers?

- hill numbers are a set of biodiversity metrics designed to standardize metrics and quantify biodiversity and richness differently depending on how we want to emphasize abundance while also accounting for differences in sampling sizes and efforts (read more about this Eric)

5) What is the advantage of using hill numbers to estimate diversity/richness?

- Chao et al. 2014: incorporating abundance into calculating diversity metrics is important for studying functionality in particular since some species that may not be as abundant as others may not contribute to an ecosystem function as much as others. At the same time rare species may be filling a specific niche or we might be concerned about exotics or at risk species.

6) Are the diversity and richness estimates calculated with hill numbers sensitive to anything, e.g., rare species/abundance, etc:

7) Find me the best example paragraph you think you read describing the use of hill numbers to estimate diversity/richness (field survey paper): _____

8) Find me the best TWO description of using GLMM to compare abundance/diversity/richness at the Corridor Project: _____

Methods:

1. add a few sentences on drying, keys used to ID, and depositing vouchers

Analyses

1. Write a short paragraph on how you calculated and compared species richness and diversity (hill numbers, glmm)-
2. Write a short paragraph on how you calculated and compared functional diversity (how you measured it, how you compared it)

Results

1. answer the overview questions, then stitch them together into a paragraph

- any species restricted to 1-2 habitat types
- Were all species found in all blocks? Were any restricted to only 1-2 blocks?
- Were all species found in the matrix? (expect that so, since it is the 'baseline' or 'source' habitat)
- Number of species in each functional group
- most common 3-4 species
- any rare species?
- any invasive / exotic species?

67 **Figures**

- 68 1. ~~Figure of species richness results.~~
- 69 2. Figure of species diversity results.
- 70 3. Figure of biomass of different (R/T/D) functional groups.
- 71 4. ~~Figure of abundance of individual species.~~
- 72 5. ~~Figure of the patch layout with pitfalls.~~

73 **Tables**

- 74 1. ~~Table: count by species by habitat.~~
- 75 2. table: results of species richness analyses.
- 76 3. table: results of species diversity analyses.
- 77 4. table: results of functional diversity analyses.

78 **Misc.**

- 79 1. Map of where field site is located.
- 80 2. Pictures of different species, sampling, field sites

INTRODUCTION

As human disturbances continue to expand into natural landscapes, intact habitats are becoming increasingly fragmented (**Diaz 2019**). Like many ecological processes, fragmentation is a complex and multifaceted phenomenon bringing about many consequences which can be both positive and negative for ecosystems (Fahrig 2003, Fletcher et al. 2018). However, as habitats are broken down community structures are significantly altered (**Laurance et al. 2018**). This alteration of structure typically leads to loss in biodiversity on a global scale and interruptions in ecosystem processes and functions (Haddad 2015).

Corridors have been shown to be an important mechanism for minimizing negative consequences of fragmentation (Haddad et al. 2003). By improving habitat structure to help facilitate dispersal, wildlife corridors inform movement dynamics of local populations and can shape land uses and occupancy (Forman 1995). Because of this dynamic it becomes necessary to understand responses by species compositions at all taxonomic levels and potential trophic cascades resulting from changes in habitat structure and connectivity (Debinski and Holt 2000).

By measuring changes in biodiversity and species richness within experimental designs we are able to isolate factors might be contributing to ecological patterns and processes (Resasco et al. 2017, Fletcher Jr. et al. 2023). Past studies have measured changes in biodiversity for many different taxa (Tewksbury et al. 2002, Collins et al. 2017, Graham et al. 2022), yet much work is still needed to build a full scope for how organisms are being effected. Furthermore it is important that we expand our knowledge on how composition changes might impact functional diversities and potential implications for the effectiveness of ecosystem services (Hevia et al. 2017).

Dung beetles have emerged as a model system with which to test spatial ecology hypotheses (Roslin 2000, Rös et al. 2012). They are an incredibly well studied group of insects which are well known for driving a multitude of ecosystem functions (Hasan et al. 2024). The removal, breakdown, and burial of animal feces drive important ecosystem interactions provided by dung beetles enhancing nutrient cycling and soil quality, the reduction of breeding sites for parasites, and a reduction in methane emissions from dung (Iwasa et al. 2015, Slade et al. 2016). Here, we aim to gain an understanding of how dung beetles, a group of insects well known for strong dispersal ability in order to compete for ephemeral resources (Hanski and Cambefort 1991), interact with corridors in their landscapes. We sampled dung beetle communities in experimental landscapes developed for the express purposes of comparing connected and isolated patches, as well as the effects of patch area to edge ratio and distance to edge (Tewksbury et al. 2002). To ask the questions: (1) How are species abundances of dung beetles distributed within isolated and connected patches and what are their relationships with assemblages in matrix habitat? (2) Does species richness vary when movement between patches is facilitated by movement corridors? (3) Are there shifts in species diversity/composition and what are the implications for ecosystem service functionality?

Paragraph 5: Here is what we did to address this unknown. *The hypotheses we tested*

Methods

Study site

Our study took place at the Savannah River Site (SRS), a National Environmental Research Park in southern South Carolina, US (33.208° N, 81.408° W) in four of seven experimental landscapes designed for the purposes of directly observing the impacts of corridors and patch shape on the movements of plants and animals (Tewksbury et al. 2002). Each experimental landscape, termed blocks, consists of four patches of open habitat around a central patch all together within a matrix of pine savanna. In each block the central patch (100 × 100 m) is always connected to one peripheral patch with identical dimensions by a 150 × 25 m corridor, this will hereafter be referred to as the connected patch. The remaining patches are either “winged” or “rectangular”. The winged patch is also 100 × 100 m, however they exhibit their characteristic wings in the form of two 75 × 25 m offshoots meant to account for the extra area and edge space the corridor provides. The rectangular patch is 100 × 137.5 m also the same area as the space of the connected patch plus the corridor. Each block has a duplicate of either the winged or rectangle patch, all peripheral patches being 150 m from the center patch. For this study sampling was done in one of each patch type and in one matrix plot per block, all matrix blocks were set up 150 m away from the center as well.

Dung beetle sampling

In the months of July and August 2024 dung beetles were sampled in 4 blocks spread across SRS, baited pitfall traps were placed in one of each patch type and in one matrix plot per block. Traps were placed in groups of 3 in the centers of each patch approximately 250 meters from the midpoint of the central patch 40 m from patch edge. Pitfalls were oriented in a triangular pattern with the bottom two traps positioned towards the center patch, each trap 20 m apart. Plots in the matrix were set up in a similar fashion with the center point 250 m from the center placed equidistant between adjacent patches. Individual pitfall traps consisted of two components, a 10cm tall by 8 cm wide cylinder base topped with a funnel with a 10cm wide rim. We sourced pig feces from the University of Florida Swine Barn Unit. Bait was processed into 5cm wide balls and wrapped in a layer of coffee filter material. For each sample period, traps were buried flush with the ground and baited with pig dung between 8-9 pm and picked up 12 hours later, all beetles captured were stored in ethanol for further processing. In total 16 sampling rounds were carried out with 4 rounds per block, 196 samples were collected.

All dung beetles were counted and identified to species as described in Nemes and Price (2015) and Edmonds (2023). Fifteen individuals of each species with adequate captures were dried to equilibrium and weighed for biomass measurements. Voucher specimens for each species will be deposited at the Florida State Collection of Arthropods.

Analyses

Biodiversity between patch types was compared using Hill numbers, a set of indexes developed with the goal of providing a unifying context for the quantification of the many ways we measure biodiversity (Jost 2006). They are an alternative to more specialized metrics such as alpha, beta, and gamma diversities while being more standardized than other indexes such as Renyi or HCDT entropies, of which both groups of metrics are less intuitive for interpretation. Hill numbers are now the preferred metric for describing community dynamics for two reasons. First, they are extrapolated from the same equation, manipulating a single parameter (i.e., q) to arrive at estimates of richness and diversity. Second, by manipulating q we can gain an understanding of compositional shifts otherwise obscured while using species richness (Chao et al. 2014). We compared community composition by increasing magnitudes of diversity components (i.e., qD) of $0D$ (i.e., species richness), $1D$ (i.e., Shannon entropy), and $2D$ (i.e., Simpson Diversity). Diversity numbers and species richness were calculated using the package `hill` (Li 2018) for the R statistical programming language (citation). Diversity numbers were calculated using package `iNEXT` (Hsieh et al. 2016). Bray-Curtis dissimilarity values were calculated using package `Vegan` (Oksanen et al. 2025). Dung beetles were assigned traits by waste removal guild and habitat preference.

To test for the effects of connectivity on abundance, species richness, and species diversity we compared the values of the Hill Shannon and Simpson indexes in the different patch types and matrix. For abundance and richness we used generalized linear mixed models (i.e., GLMM) fitted to a poisson distribution (**bolker citation?**). Compared (1) the overall species richness and (2) the abundance of the top 6 most common species in each patch type. We included the identity of the sampling block as a random effects. To model our diversity metrics we took a similar approach, but this time using GLMMs with a Gaussian distribution (**citation**). All models were fit using `lme4` package (Bates et al. 2015). Prior to conducting our modeling we evaluated the suitability of our data with `qqplots` generated with the `DARMA` package (**citation**).

RESULTS

Overview: Community Composition and Abundance

Overall, I collected $N = 5213$ dung beetles belonging to $N = 16$ species. The $N = 6$ species comprised of 93.9% of all captures: *Canthon vigilans* ($N = 1473$), *Ateuchus lecontei* ($N = 1115$), *Phanaeus igneus* ($N = 958$), *Aphodius alloblackburneus* ($N = 585$), *Dichotomius carolinus* ($N = 556$), and *Onthophagus pennsylvanicus* ($N = 207$; Table 1). All but four species were captured in every patch type. *Onthophagus concinnus* was only found in the matrix and winged patches, while *Onthophagus striatulus* was only captured in matrix habitat and rectangular patches. *Geotrupes blackburnii* and *Onthophagus tuberculifrons* were the only species restricted to one patch type (winged and matrix, respectively). All species were within their native ranges.

When comparing the total abundance of beetles (all species combined) across patch types, there were no significant difference with one exception: fewer individuals were captured in rectangular patches ($P < 2e-6$). Statistical analysis of abundance focused on the six most abundant species. When looking at counts for our most abundant species, results were variable but overall follow a consistent pattern where the most individuals of a given species are more frequent in the matrix then corridor and winged patches with a dip at the rectangle patch. One difference to note is that *Aphodius alloblackburneus* had much higher counts in matrix patches in contrast to other patch types.

Species Richness

The number of species per patch varied from $N = 8$ (rectangle patch in block 8) to $N = 13$ (matrix patch in block 53N). Species richness was relatively even across patch types with matrix and connected patches averaging out to approximately $N = 11$ species and rectangle and winged patches averaging to approximately $N = 10$ species. Overall there were no significant effects, however species richness patterns were variable between sampling blocks.

Species Diversity

Values for Hill numbers showed no patterns for shifts in species composition by patch type. Data for Shannon diversity showed no differences in the distribution of rare species between patch types. On average connected patches had a value of $D = 5.29$, while mean estimates for all other patches remained close with $+0.03\%$ for rectangle, -0.02% for matrix, and -0.06% for winged patches. There was no significance between patch types but data was highly variable between patch types and sampling blocks.

Values for Simpson Diversity also showed no differences but instead for more abundant species composing the dung beetle assemblages. Simpson diversity had a mean value of $D = 4.07$ in the connected patch, also with other values in close proximity with matrix $+0.02\%$, rectangle $+0.04\%$, and winged at -0.1% . There was no significant difference between patch types, however this data was also highly variable between patch type and sampling blocks.

Functional Diversity

DISCUSSION

Recap main goals into findings

This study shows that while habitat type may have an impact on the individual abundances of dung beetles, the arrangement of individuals show little difference as a result of the presence of movement corridors. Past studies have shown similar trends where habitat type and forest regeneration stages are key in the partitioning of dung beetle assemblages (Arellano et al. 2008, Bitencourt and Silva 2016, Conover et al. 2019). This is further supported by the fact that capture rates were lowest in the rectangular patch, the treatment with the least edge to area ratio, suggesting that dung beetles in the matrix act as a source population which feeds into open patches through habitat edge.

While we did not detect any patterns of species richness between patch types in our modeling,

i want to look back at rarefied richness, was sampling complete in each patch?

A comparison of total species richness per patch type per block shows that the sampling plot with the most total species captured was in the matrix.

Analysis of Hill numbers indicated that species compositions were even between patch types. Comparing values of Simpson's Diversity between patches determined that dominant species were not prevalent in any one treatment type. Likewise, the Shannon index values insisted that rare species throughout the study population were even.

here write about low sample sizes and reasons for why dung beetle communities would be so similar across treatment types. Dispersal, scale (roslin), maybe again a good reason to expect matrix as a source pop.

The total number of dung beetle species captured $N = 16$ and the total individuals $N = 5213$ are similar to those in studies conducted in similar habitats and regions of the US (Nealis 1977, Conover et al. 2019, Stanbrook and King 2022).

revisit bray curtis

1. Abundances in matrix vs connected patch and why this could be happening

- source pop to habitat edge

2. species richness again supporting that matrix is more of an ideal habitat for dung beetle community

3. diversity indices community structures weren't highly different between patch types

4. bray curtis hinting at similar land uses between corridor and winged patch

- like julians paper corridors benefit certain populations and more fit populations are able to make better use

Interpretation of results

1. Abundance

- reason for highest abundances in matrix and connected patch
- lower abundance in rectangle hinting at fragmentation effects

2. Species Richness & Diversity

- the role of habitat connectivity in shaping community structure or lack thereof
- why do we think connected had lowest species richness??

3. Functional traits and ecological impacts

- did corridors favor a functional trait
- why might there be a trait response
- implications for ecosystem processes
- like dung removal papers seed dispersal and yep

4. Comparing to previous studies

- how are things aligning
- think about the biology

5. Limitations and future work

- potential confounding factors (seasonality, distance from edge, sampling methodology and temporal variation)
- other directions to go (dispersal -> radar, specifically measuring changes in ecosystem services)

6. Takeaways for conservation and management

- dung beetles are robust
- what do think about corridor design and considerations for fragmented landscapes
- practical applications think about the beetles

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FIGURES & TABLES

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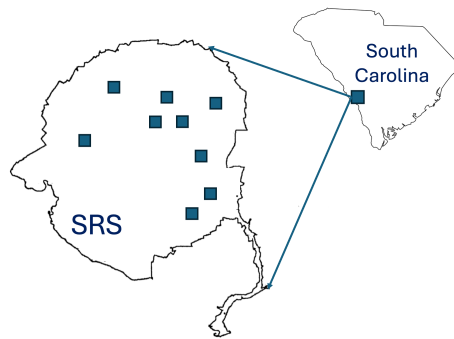


Figure 1: Experimental block with the different patches and distance between them.

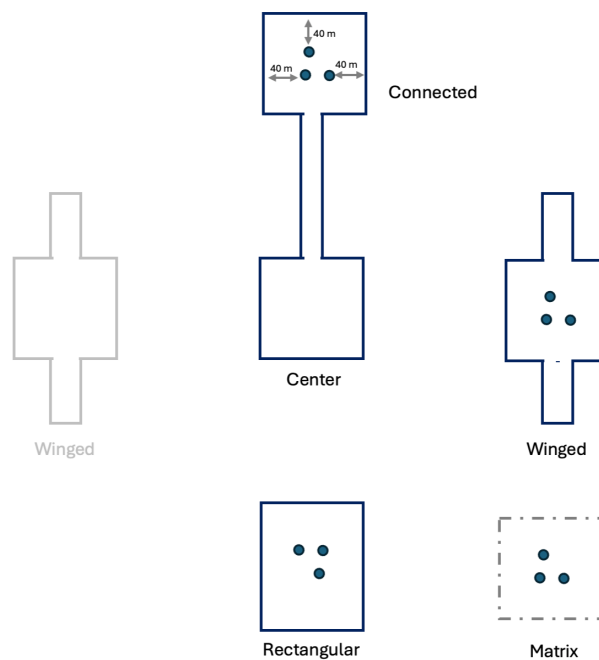


Figure 2: Experimental block with the different patches and distance between them.

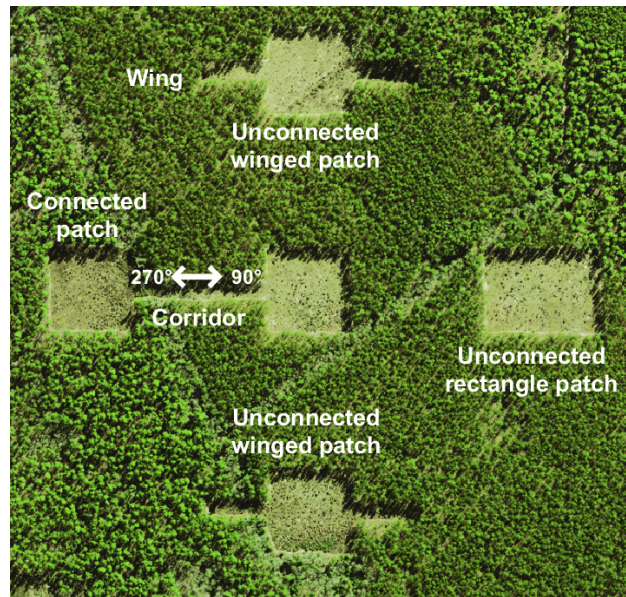


Figure 3: Experimental block with the different patches and distance between them.

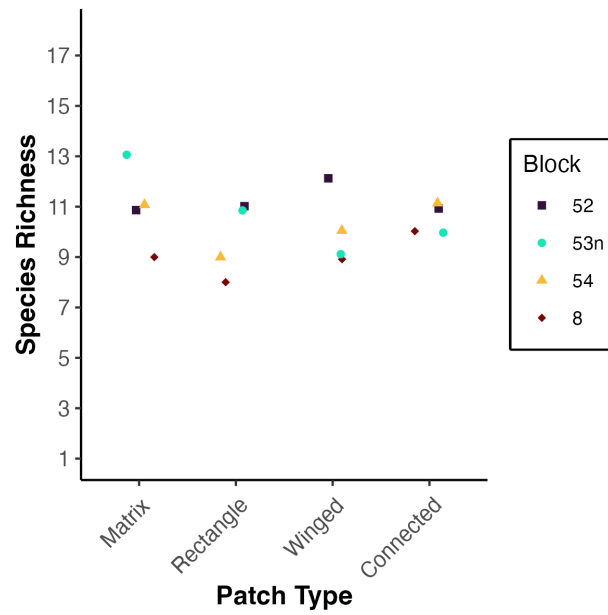


Figure 4: Dung beetle species richness in three different — and the forest matrix surrounding patches.

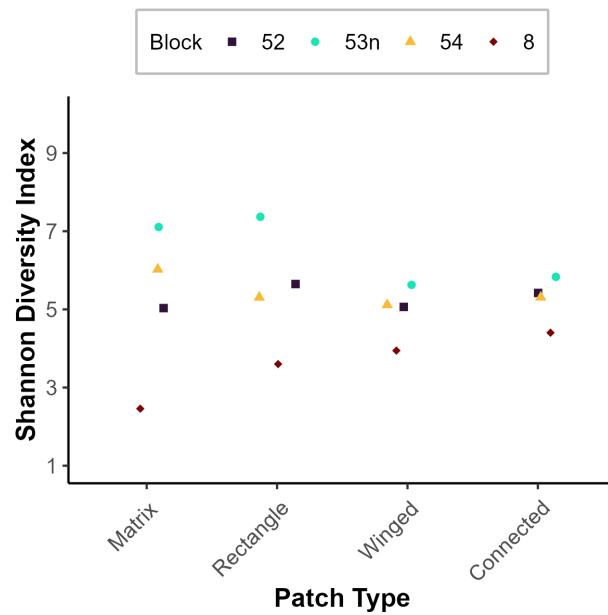


Figure 5: Dung beetle Shannon diversity in three different — and the forest matrix surrounding patches.

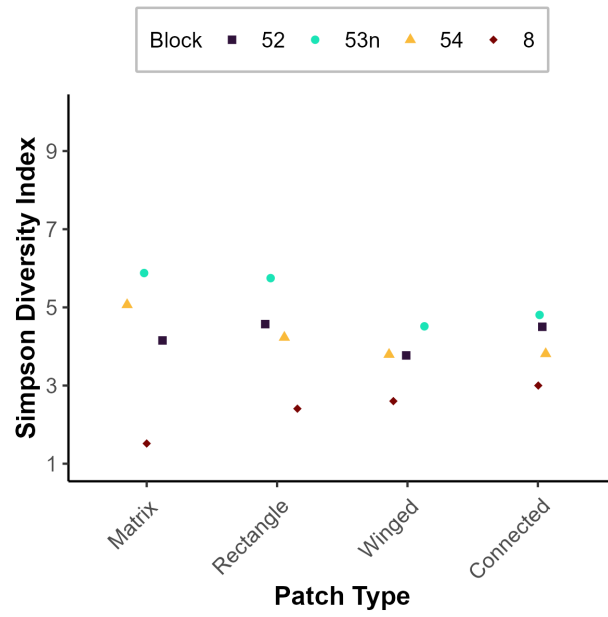


Figure 6: Dung beetle Simpson's index in three different — and the forest matrix surrounding patches.

Table 1: Dung beetle species sampled in the SRS site and their total abundance over the course of the study.

Species	Guild	N	Matrix	Corridor	Winged	Rectangular
<i>Canthon vigilans</i>	roll	1473	x	x	x	x
<i>Ateuchus lecontei</i>	tunnell	1115	x	x	x	x
<i>Phanaeus igneus</i>	tunnell	958	x	x	x	x
<i>Dichotomius carolinus</i>	tunnell	556	x	x	x	x
<i>Aphodius alloblackburneus</i>	dwell	585	x	x	x	x
<i>Onthophagus pennsylvanicus</i>	tunnell	207	x	x	x	x
<i>Melanocanthon bispinatus</i>	roll	83	x	x	x	x
<i>Phanaeus vindex</i>	tunnell	133	x	x	x	x
<i>Boreocanthon probus</i>	roll	47	x	x	x	x
<i>Copris minutus</i>	tunnell	24	x	x	x	x
<i>Deltochilum gibbosum</i>	roll	14	x	x	x	x
<i>Aphodius oximus</i>	dwell	11	x	x	x	x
<i>Geotrupes blackburnii</i>	tunnell	1			x	
<i>Onthophagus concinnus</i>	tunnell	2	x		x	
<i>Onthophagus striatulus</i>	tunnell	3	x			x
<i>Onthophagus tuberculifrons</i>	tunnell	1	x			

Table 2: Total dung beetles captured in all replicates of a patch type.

patch	n
Corridor	1359
Matrix	1713
Rectangle	942
Winged	1199

Table 3: AOV TABLE CAPTION

term	statistic	df	p.value
patch_type	73.415	3	0

OTHER REQUIRED TEXT

Dedication

To my family who never stopped supporting me along this journey, my friends who kept me company along the way, and my mentors at VCU who believed in me before I did myself.

List of Abbreviations

1. SRS: Savannah River Site.
2. Another word: And the list continues with another definition.

Biographical Sketch

Eric Escobar-Chena completed his Bachelors education at Virginia Commonwealth University in 2023. During his time there he developed a fondness for insects which grew into a curiosity of the natural world. He later began to explore this curiosity deeper in beginning his graduate education at the University of Florida as a Master's Student under the supervision of Emilio Bruna.

Text Sandbox

As human disturbances continue to expand into natural landscapes, intact habitats are becoming increasingly fragmented. This degradation lends to loss in biodiversity on a global scale and interruptions in ecosystem processes and functions (Haddad 2015). Effects from isolation can vary, however as habitats are broken down community structures are significantly altered (Laurance et al. 2018). Corridors have been shown to be an important mechanism for facilitating the movement of organisms through fragmented landscapes with the goal of minimizing negative consequences of fragmentation (Haddad et al. 2003). As disturbance continues to intensify, it is becoming increasingly more important to understand how different taxonomic groups. Here, we aim to gain an understanding of how dung beetles, a group of insects well known for strong dispersal ability in order to compete for ephemeral resources (Hanski and Cambefort 1991), interact with corridors in their landscapes.

Dung beetles have emerged as a model system with which to test spatial ecology hypotheses (Roslin 2000, Rös et al. 2012). They are an incredibly well studied group of insects which are well known for driving a multitude of ecosystem functions (Hasan et al. 2024). The removal, breakdown, and burial of animal feces drive important ecosystem interactions provided by dung beetles enhancing nutrient cycling and soil quality, the reduction of breeding sites for parasites, and a reduction in methane emissions from dung (Iwasa et al. 2015, Slade et al. 2016). Local assemblages of dung beetles can be species-rich with species comprising a broad range of functional traits (e.g., size, foraging style, resource-use) (**WOS:000891747700001?**). Previous studies have shown that isolated patches of habitat frequently have lower dung beetle diversity and abundance than areas of continuous habitat, as well as documented their presence in linear strips of habitat that resemble corridors (Gray et al. 2022). Past studies have also focused on how landscape structure alters the community compositions of dung beetles (Costa et al. 2017), yet large landscape scale experimental studies with carefully controlled and replicated treatments are non-existent for this model species.

Here, we aim to determine how connectivity and fragmentation affect Species Richness and Diversity, Abundance, and functional diversity. We sampled dung beetle communities in experimental landscapes developed for the express purposes of comparing connected and isolated patches, as well as the effects of patch to edge ratio and distance to edge. To ask the question of (1) how landscape connectivity impacts dung beetle assemblages dung beetles were collected, identified, and counted with the expectation that biodiversity and abundance would be higher in patches connected by corridors. Additionally we asked (2) Are corridors benefiting any one functional trait over another? Since our experimental system consists of open habitats amongst a forested matrix, we anticipate that species preferring open areas and generalists may be more common in our sampling.