

Contents

TO DO LIST	1
INTRODUCTION	9
Methods	10
RESULTS	13
DISCUSSION	14
REFERENCES	19
FIGURES & TABLES	22
Text Sandbox	38

TO DO LIST

FOR TOMORROW:

- 1) Finish adding citations
- 2) Stat results: biology first, then stats (e.g., abundance ranged from xxx in rectangular to xxx in winged)
- 3) Review other papers to find:
 - those with similar results
 - those with contrary results
 - do this with dung beetles AND other insect taxa

DOWN THE ROAD

- 1) **Results:** Did you get any species not captured in other long-leaf/SE USA forest sites?
- 2) **Methods:** Find me the best example paragraph you think you read describing the use of hill numbers to estimate diversity/richness (field survey paper)
- 3) **Methods:** Find me the best TWO descriptions of using GLMM to compare abundance/diversity/richness at the Corridor Project
- 4) **Methods:** Write a short paragraph on how you calculated and compared functional diversity (how you measured it, how you compared it)
- 5) **Figure:** biomass of different (R/T/D) functional groups.
- 6) **Table:** Results of functional diversity analyses.

THE INFLUENCE OF CONNECTIVITY ON DUNG BEETLE COMMUNITIES

By

ERIC ESCOBAR-CHENA

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2025

© 2025 Eric Escobar-Chena

To my mom, dad, and two sisters. This thesis is a chapter in our immigrant story.

ACKNOWLEDGMENTS

We thank the USDA Forest Service for maintaining experimental landscapes and assisting in getting established at the site. I also wanted to specifically thank Thomas Smith for his help in data collection, Sara Escobar-Chena for her help in processing and data entry.

LIST OF ABBREVIATIONS

SRS: Savannah River Site.

GLMM: Generalized Linear Mixed Model

Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science.

THE INFLUENCE OF CONNECTIVITY ON DUNG BEETLE COMMUNITIES

By

Eric Escobar-Chena

August 2025

Chair: Emilio Bruna

Major: Wildlife Ecology and Conservation

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.

CHAPTER 1

THE INFLUENCE OF CONNECTIVITY ON DUNG BEETLE COMMUNITIES

INTRODUCTION

As human disturbances continue to expand into natural landscapes, intact habitats are becoming increasingly fragmented (Taubert et al. 2018, Díaz et al. 2019, Ma et al. 2023). 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 (Haddad et al. 2003, Jennings and Tallamy 2006, Laurance et al. 2018). This alteration of structure typically lends 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). The resulting changes in species composition are important to identify because any species impacted would have corresponding effects depending on how they interact with the ecosystem (Zhou et al. 2023). Any gain or loss in key members of an community could disrupt processes which on their own could shape ecosystems (Cuke and Srivastava 2016), or effect other organisms which rely on said interaction (Wu et al. 2011). 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).

[EB edit: break this next sentence into 3 to carry reader though the logic: changes in species diverstiy are important to understand because species are involved in interactions. If we gain or lose species we could gain or lose interactions and resulting ecosystems processes. there is some evidence of this, but... look at the green text notes below]

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 endeavored to experimentally measure changes in community compositions as a result of connecting habitats with corridors (Tewksbury et al. 2002, Collins et al. 2017, Graham et al. 2022) **here fix citations**, yet very few have directly compared matrix and patch populations. **examples of dispersal concepts (drift fence etc** Land use is different from one species to another so it is vital to

understand where compositions are distributed and what processes might be driving population differences.

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 (Nichols et al. 2008, Iwasa et al. 2015, Slade et al. 2016). **[EB edit: I added the following to justify dung beetles more, and then made the questions a second paragraph]** 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, (Ospina-Garcés et al. 2018, deCastro-Arrazola et al. 2023)]. 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 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?

Methods

Study site

Our study took place at the Savannah River Site (SRS), a National Environmental Research Park in southern South Carolina, USA (33.208° N, 81.408° W, Figure 1). 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 (Figure 2). 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 (Figure 3). 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 (Posit team 2025). 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 et al. 2009). 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 linear mixed effects models with a Gaussian distribution (Chao et al. 2014). In all models, the reference level for patch type was Matrix. All models were fit using `lme4` package (Bates et al. 2015). Prior to conducting our modeling we evaluated the the suitability of our data with *qqplots* generated with the `DARMA` package (Hartig 2024).

We used linear mixed-effects models to compare the influence of patch type on both Shannon Diversity and Simpson’s indexes, including block as a random effect to account for spatial variation. Across both diversity models, the block-level random effect standard deviation was slightly greater than the residual error, indicating that variation between blocks accounted for a substantial portion of the overall variability.

RESULTS

Overall, I collected $N = 5213$ dung beetles belonging to $N = 16$ species. The $N = 6$ most dominant 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.

Beetle Abundance

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 ($\beta = -0.402$, $P < 0.001$, Table 4).

Statistical analysis of abundance focused on the six most abundant species. A generalized linear mixed model identified significant effects for both species ID and patch type on dung beetle abundance (Table 7). The baseline abundance corresponds to the abundance of *Aphodius alloblackburneus* in connected patches. Compared to this baseline, *Canthon vigilans*, *Ateuchus lecontei*, and *Phanaeus igneus* showed significantly higher abundance ($\beta = 1.05, 0.73, 0.66$ respectively; all $p < 0.001$), while *Onthophagus pennsylvanicus* had lower abundance ($\beta = -0.80$, $p < 0.001$).

Species-patch interactions indicated species specific responses to treatments. In matrix plots, the positive effect on abundance was reduced for all other species (e.g., $cvig \times Matrix \beta = -0.59$, $p < 0.001$). *Ateuchus lecontei* and *Phanaeus igneus* showed increased effect on abundance in rectangle patches relative to expectations ($\beta = 0.40$ and 0.47 , respectively; $p < 0.05$). Random effects indicated moderate variability among blocks (standard deviation of intercept = 0.51).

Beetle Richness and Diversity

Plotting species richness by patch type reveals consistent richness across patch types with some variation between sampling blocks (Figure 5). The number of species per patch varied from $N = 8$ (rectangle patch in block 8) to $N = 13$ (matrix patch in block 53N). Modeling the effect of patch type on species richness with

block as a random effect determined there was no significant differences among patch types. Comparing treatments using connected patches as a baseline resulted in no significant differences in matrix ($\beta = 0.05$, $p = 0.83$), rectangle ($\beta = -0.07$, $p = 0.74$), and winged patches ($\beta = -0.05$, $p = 0.83$).

For Shannon Diversity, the estimated mean in Connected patches was 5.29 (SE = 0.66, $t = 7.95$). None of the alternative patch types showed statistically significant differences compared to Connected: Matrix ($\beta = -0.085$, SE = 0.50, $t = -0.17$), Rectangle ($\beta = 0.15$, SE = 0.50, $t = 0.30$), or Winged ($\beta = -0.34$, SE = 0.50, $t = -0.68$). Similarly, for Simpson's Diversity, the average value in Connected patches was 4.07 (SE = 0.64, $t = 6.37$). Again, none of the other patch types had significant effects: Matrix ($\beta = 0.11$, SE = 0.41, $t = 0.26$), Rectangle ($\beta = 0.17$, SE = 0.41, $t = 0.40$), and Winged ($\beta = -0.37$, SE = 0.41, $t = -0.91$).

DISCUSSION

NEED

1. rarefaction curves
2. add biomass to table 1
3. add totals of habitat in table 2 to table 1.

OUTLINE

Paragraph 1: Overview: While there may indeed be effects of patch area and connectivity on dung beetle abundance on community composition, other (landscape-scale) drivers appear to be more important.

This study advances our understanding of the factors shaping dung beetle community composition in temperate regions of the southeastern United States. In addition, the experimental design enables direct comparisons between populations in continuous matrix habitat and those in both isolated and corridor connected patches. Our main findings emphasized: (1) Habitat type and patch shape were the main driving factors for dung beetle species abundances were composed, however effects were species specific. (2) Patch shape and isolation had less of an influence on species richness which was relatively even on both a patch and block level. (3) Species diversity metrics were also relatively even across patch types however varied widely by sampling blocks. These results suggest that while there may indeed be effects of patch structure and connectivity on dung beetle abundances and community composition, other landscape scale drivers appear to be more prominent for species richness and diversity.

Paragraph 2: Effects of Edge vs. Connectivity

In comparing patc

- corridors vs. drift fence; predicted effects of body size and habitat preference
- important difference from previous drift fence studies: ours has both passive drift effects AND directed movement towards dung

- by laying out the same amount of dung in traps in all patch types, we eliminated the potential confounding effects of resource levels and abundance (sensu nick butterfly paper). Our results therefore reflect the effects of patch area / isolation / block rather than background abundance.

Paragraph 3: What then are the drivers of dung beetle diversity and abundance?

- if not area, edge, or connectivity...what are we (and maybe others) missing? Block effects suggest something at much larger scales. Potential hypotheses:
 - a) *landscape-scale variation in abundance of large mammals (deer, hogs) at SRS.* Primary dung sources likely to be deer (?), wild hogs (?), maybe gopher tortoise, coyote, and fox (?). Is anything known about the abundance of these at the SRS site, either in patches or at the block level?
 - b) *matrix permeability/structure/canopy cover* Is the matrix denser around patches where captures were lower?
 - c) *gradients in soil moisture/compaction/quality* (related to breeding)
 - d) *land-use history / legacy of ag / road proximity* (looping around to mammal abund)

Paragraph 4: That said, there were some interspecific differences in abundance.

- What are they and what could be behind them?

Paragraph 5: Our results largely echo/contrast with previous ones from the SRS and elsewhere

- example 1:
- example 2:
- example 3:

Paragraph 6: Caveats

- potential effects of seasonality
- Sampling wasn't designed to look for potential effects of edge proximity, and so we couldn't test for previously observed pattern of generalist/opportunistic species more common near edges.
- used great bait, but possible some species (eg specialists) not attracted

Paragraph 7: Moving forward

- tough to compare when most of the work has been done in the tropics; surprisingly few studies of this species-rich and ecologically vital guild in the SE US. "Despite ample work documenting their ecological importance, there is a surprising lack of research on dung beetle diversity and corridors outside of the tropics. That said, tropical studies find stark contrast between fragments/pasture. They have been found to use corridors, but it is..."
- experimental approaches to track movement and distinguish beetles already in patches vs. those coming from outside. Our preliminary data with MRR indicates individuals do move through corridors.

Paragraph 8: Close with takeaways for conservation and management

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

A few things to consider incorporating

- ellen wind paper/ connectivity

This study advances our understanding of the factors shaping dung beetle community composition in temperate regions of the southeastern United States. In addition, the experimental design enables direct comparisons between populations in continuous matrix habitat and those in both isolated and corridor connected patches. Our main findings emphasized: (1) Habitat type and patch shape were the main driving factors for dung beetle species abundances were composed, however effects were species specific. (2) Patch shape and isolation had less of an influence on species richness which was relatively even on both a patch and block level. (3) Species diversity metrics were also relatively even across patch types however varied widely by sampling blocks. These results suggest that dung beetle species are fully capable of permeating fragmented landscapes and that habitat type and connectivity shape community compositions, but landscape effects of a larger scale are driving changes in biodiversity.

Abundance

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).

Dung beetle abundances were significantly lowest in rectangular patches. Matrix patches had the most total beetles collected and consistently had the highest counts for the most dominant species. However abundances were not significantly different between matrix, connected, and winged patches. This may suggest that isolation is leading to a decrease in abundances, but it is more likely that populations in the matrix are acting as a source, and since connected and winged patches have higher edge to area ratios dung beetles were more likely to move into those patches. Past studies have shown 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) which supports why we might see these differences in local populations. In addition distance from habitat edge has been attributed to differences in spillover from source populations (Gray et al. 2022), emphasizing the importance of habitat edge in the context of our study.

We also observed that patch effects were not equally proportional for all species. The abundances of all dominant species were positively influenced by matrix habitat, but *Aphoidius alloblackburneae* responded more positively than any other species. *Phanaeus igneus* and *Ateuchus lecontei* also had higher positive effects in rectangle patches.

Richness

While abundances were different between patch types, we did not detect any patterns of species richness in our modeling. Total species counts were very even across patch types and sampling blocks. This difference indicates that even though habitat type or landscape features are informing occupational preferences, land use is more or less the same between patches and matrix. This differs from past work where species richness is lower in forest fragments (Estrada and Coates-Estrada 2002)

Diversity

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. However, for both metrics, values varied greatly by sampling blocks. Similar to our richness results this suggests that variation between patch and matrix is not distinct enough to limit the land use of dung beetles within our study site.

In contrast to what we observed with species richness it appears that assemblages larger landscape patterns are effecting the composition of assemblages across the study site.

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.

notes that are important for discussion

- habitat preference and seasonality (conover 2019, nealis 1977) > - 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
- habitat again but only part of variation form habitat specifically aphodius also phenology (roslin 2001)
- spatial scales (roslin 2000)
- morphology
 - 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.
- functionality especially gas emissions (slade 2016)
- species id and functionality (slade 2017)
- faovored species dominating in fragments (resasco 2014)
- wind direction in corridors (damschen 2014)

revisit bray curtis

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

- source pop to habiitat 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

REFERENCES

- Arellano, L., J. L. Leon-Cortes, and G. Halffter. 2008. Response of dung beetle assemblages to landscape structure in remnant natural and modified habitats in southern Mexico. *INSECT CONSERVATION AND DIVERSITY* 1:253–262.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67:1–48.
- Bitencourt, B. S., and P. G. da Silva. 2016. Forest regeneration affects dung beetle assemblages (Coleoptera: Scarabaeinae) in the southern Brazilian Atlantic Forest. *JOURNAL OF INSECT CONSERVATION* 20:855–866.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135.
- Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84:45–67.
- Collins, C. D., C. Banks-Leite, L. A. Brudvig, B. L. Foster, W. M. Cook, E. I. Damschen, A. Andrade, M. Austin, J. L. Camargo, D. A. Driscoll, R. D. Holt, W. F. Laurance, A. O. Nicholls, and J. L. Orrock. 2017. Fragmentation affects plant community composition over time. *Ecography* 40:119–130.
- Conover, D., J. Dubeux, and X. Martini. 2019. Phenology, Distribution, and Diversity of Dung Beetles (Coleoptera: Scarabaeidae) in North Florida’s Pastures and Forests. *Environmental Entomology* 48:847–855.
- Costa, C., V. H. F. Oliveira, R. Maciel, W. Beiroz, V. Korasaki, and J. Louzada. 2017. Variegated tropical landscapes conserve diverse dung beetle communities. *PEERJ* 5.
- Cuke, M., and D. S. Srivastava. 2016. Divergent effects of tropical forest fragmentation and conversion on leaf litter decomposition. *LANDSCAPE ECOLOGY* 31:1037–1050.
- Debinski, D. M., and R. D. Holt. 2000. A Survey and Overview of Habitat Fragmentation Experiments. *Conservation Biology* 14:342–355.
- deCastro-Arrazola, I., N. R. Andrew, M. P. Berg, A. Curtsdotter, J.-P. Lumaret, R. Menéndez, M. Moretti, B. Nervo, E. S. Nichols, F. Sánchez-Piñero, A. M. C. Santos, K. S. Sheldon, E. M. Slade, and J. Hortal. 2023. A trait-based framework for dung beetle functional ecology. *Journal of Animal Ecology* 92:44–65.
- Díaz, S., J. Settele, E. S. Brondízio, H. T. Ngo, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. R. Chowdhury, Y.-J. Shin, I. Visseren-Hamakers, K. J. Willis, and C. N. Zayas. 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* 366:eaax3100.
- Edmonds, W. D. 2023. Taxonomic review of the North American dung beetle genus *Melanocanthon* Halffter, 1958 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltotilini). *Insecta Mundi*.
- Estrada, A., and R. Coates-Estrada. 2002. Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. *BIODIVERSITY AND CONSERVATION* 11:1903–1918.
- Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515.
- Fletcher Jr., R. J., T. A. H. Smith, N. Kortessis, E. M. Bruna, and R. D. Holt. 2023. Landscape experiments unlock relationships among habitat loss, fragmentation, and patch-size effects. *Ecology* 104:e4037.
- Fletcher, R. J., R. K. Didham, C. Banks-Leite, J. Barlow, R. M. Ewers, J. Rosindell, R. D. Holt, A. Gonzalez, R. Pardini, E. I. Damschen, F. P. L. Melo, L. Ries, J. A. Prevedello, T. Tscharnke, W. F. Laurance, T. Lovejoy, and N. M. Haddad. 2018. Is habitat fragmentation good for biodiversity? *Biological Conservation* 226:9–15.
- Forman, R. T. T. 1995. Some general principles of landscape and regional ecology. *Landscape Ecology* 10:133–142.
- Graham, C. D. K., C. R. Warneke, M. Weber, and L. A. Brudvig. 2022. The impact of habitat fragmentation on domatia-dwelling mites and a mite-plant-fungus tritrophic interaction. *Landscape Ecology* 37:3029–3041.

- Gray, R. E. J., L. F. Rodriguez, O. T. Lewis, A. Y. C. Chung, O. Ovaskainen, and E. M. Slade. 2022. Movement of forest-dependent dung beetles through riparian buffers in Bornean oil palm plantations. *JOURNAL OF APPLIED ECOLOGY* 59:238–250.
- Haddad, N. M. 2015, March. Habitat fragmentation and its lasting impact on Earth’s ecosystems | Science Advances.
- Haddad, N. M., D. R. Bowne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent, and T. Spira. 2003. CORRIDOR USE BY DIVERSE TAXA. *Ecology* 84:609–615.
- Hanski, I., and Y. Cambefort. 1991. *Dung Beetle Ecology*. Princeton University Press.
- Hartig, F. 2024. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.
- Hasan, F., K. J. Wallace, S. V. Fowler, L. A. Schipper, Z. Hemmings, J. D. Berson, and A. D. Barnes. 2024. Dung beetles drive direct and indirect changes in ecosystem multifunctionality. *Functional Ecology* 38:1971–1983.
- Hevia, V., B. Martín-López, S. Palomo, M. García-Llorente, F. de Bello, and J. A. González. 2017. Trait-based approaches to analyze links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges. *Ecology and Evolution* 7:831–844.
- Hsieh, T. C., K. H. Ma, and A. Chao. 2016. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* 7:1451–1456.
- Iwasa, M., Y. Moki, and J. Takahashi. 2015. Effects of the activity of coprophagous insects on greenhouse gas emissions from cattle dung pats and changes in amounts of nitrogen, carbon, and energy. *ENVIRONMENTAL ENTOMOLOGY* 44:106–113.
- Jennings, V. H., and D. W. Tallamy. 2006. Composition and Abundance of Ground-Dwelling Coleoptera in a Fragmented and Continuous Forest. *Environmental Entomology* 35:1550–1560.
- Jost, L. 2006. Entropy and diversity. *Oikos* 113:363–375.
- Laurance, W. F., J. L. C. Camargo, P. M. Fearnside, T. E. Lovejoy, G. B. Williamson, R. C. G. Mesquita, C. F. J. Meyer, P. E. D. Bobrowiec, and S. G. W. Laurance. 2018. An Amazonian rainforest and its fragments as a laboratory of global change. *BIOLOGICAL REVIEWS* 93:223–247.
- Li, D. 2018. hillR: Taxonomic, functional, and phylogenetic diversity and similarity through Hill Numbers. *Journal of Open Source Software* 3:1041.
- Ma, J., J. Li, W. Wu, and J. Liu. 2023. Global forest fragmentation change from 2000 to 2020. *Nature Communications* 14:3752.
- Nealis, V. G. 1977. Habitat associations and community analysis of South Texas dung beetles (Coleoptera: Scarabaeinae). *Canadian Journal of Zoology* 55:138–147.
- Nemes, S. N., and D. L. Price. 2015. Illustrated Keys to the Scarabaeinae (Coleoptera: Scarabaeidae) of Maryland. *Northeastern Naturalist* 22:318–344.
- Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amezcuita, and M. E. Favila. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* 141:1461–1474.
- Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O’Hara, P. Solymos, M. H. H. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. D. Caceres, S. Durand, H. B. A. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. O. Hill, L. Lahti, D. McGlinn, M.-H. Ouellette, E. R. Cunha, T. Smith, A. Stier, C. J. F. T. Braak, J. Weedon, and T. Borman. 2025. *Vegan: Community Ecology Package*.
- Ospina-Garcés, S. M., F. Escobar, M. L. Baena, A. L. V. Davis, and C. H. Scholtz. 2018. Do dung beetles show interrelated evolutionary trends in wing morphology, flight biomechanics and habitat preference? *Evolutionary Ecology* 32:663–682.
- Posit team. 2025. *RStudio: Integrated Development Environment for R*. Posit Software, PBC, Boston, MA.
- Resasco, J., E. M. Bruna, N. M. Haddad, C. Banks-Leite, and C. R. Margules. 2017. The contribution of theory and experiments to conservation in fragmented landscapes. *Ecography* 40:109–118.
- Rös, M., F. Escobar, and G. Halffter. 2012. How dung beetles respond to a human-modified variegated landscape in Mexican cloud forest: A study of biodiversity integrating ecological and biogeographical perspectives. *Diversity and Distributions* 18:377–389.
- Roslin, T. 2000. Dung beetle movements at two spatial scales. *Oikos* 91:323–335.
- Slade, E. M., T. Roslin, M. Santalahti, and T. Bell. 2016. Disentangling the “brown world’ faecal-detritus interaction web: Dung beetle effects on soil microbial properties. *Oikos* (Copenhagen, Denmark) 125:629–635.

- Stanbrook, R., and J. R. King. 2022. Dung beetle community composition affects dung turnover in subtropical US grasslands. *Ecology and Evolution* 12:e8660.
- Taubert, F., R. Fischer, J. Groeneveld, S. Lehmann, M. S. Müller, E. Rödiger, T. Wiegand, and A. Huth. 2018. Global patterns of tropical forest fragmentation. *Nature* 554:519–522.
- Tewksbury, J. J., D. J. Levey, N. M. Haddad, S. Sargent, J. L. Orrock, A. Weldon, B. J. Danielson, J. Brinkerhoff, E. I. Damschen, and P. Townsend. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences* 99:12923–12926.
- Wu, X., J. E. Duffy, P. B. Reich, and S. Sun. 2011. A brown-world cascade in the dung decomposer food web of an alpine meadow: Effects of predator interactions and warming. *Ecological Monographs* 81:313–328.
- Zhou, G., Y. Huan, L. Wang, Y. Lan, T. Liang, B. Shi, and Q. Zhang. 2023. Linking ecosystem services and circuit theory to identify priority conservation and restoration areas from an ecological network perspective. *Science of The Total Environment* 873:162261.

FIGURES & TABLES

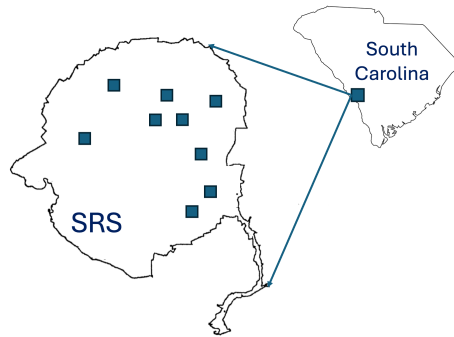


Figure 1: Experimental block with the different patches and distance between them.

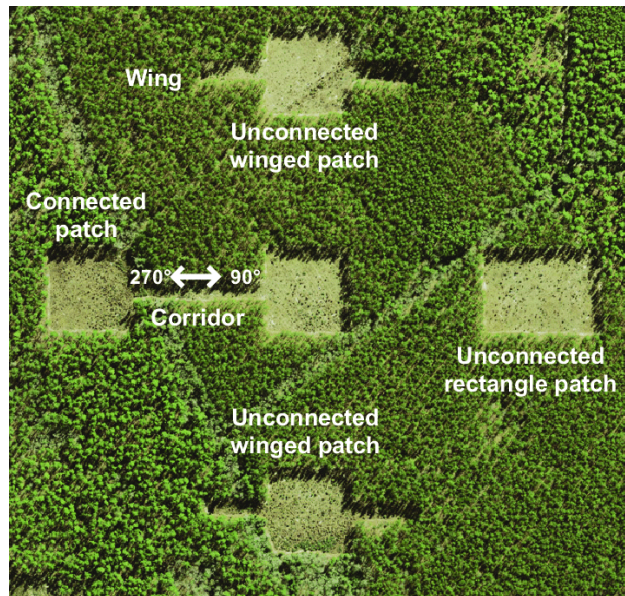


Figure 2: Experimental block with the different patches and distance between them.

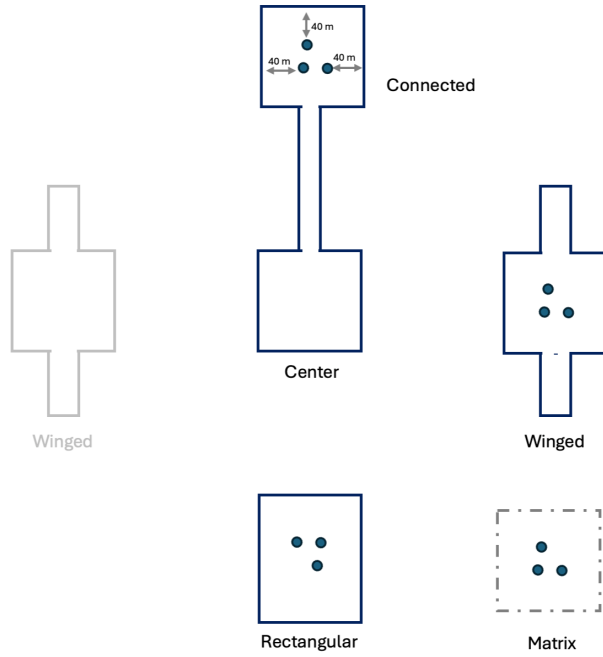


Figure 3: Experimental block with the different patches and distance between them.

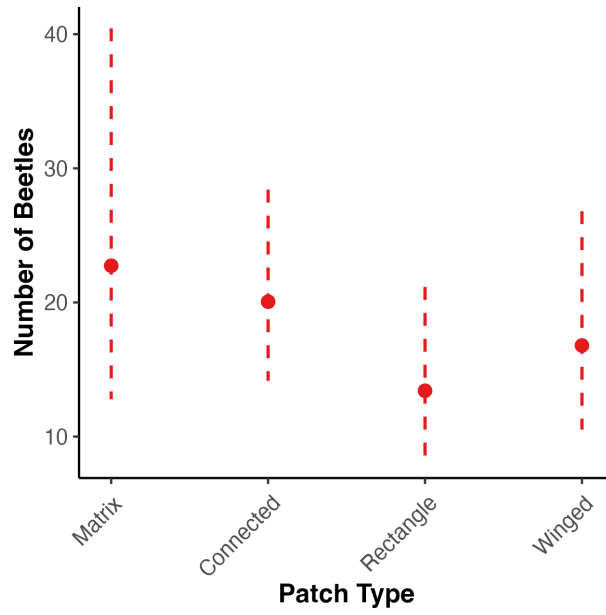


Figure 4: Dung beetle abundance in three different — and the forest matrix surrounding patches.

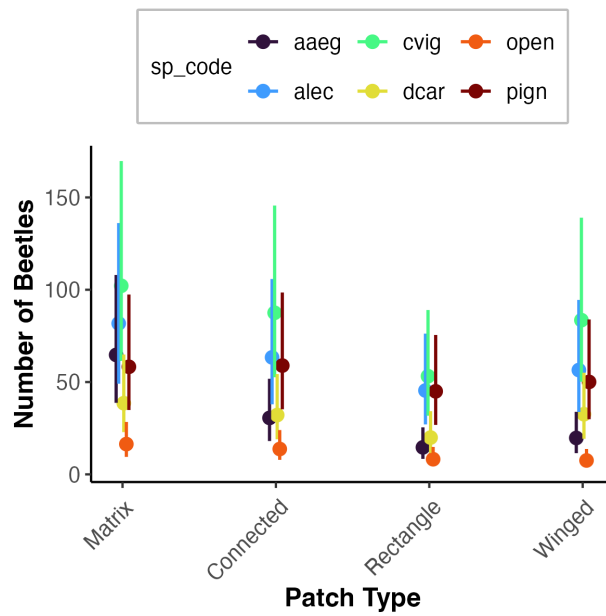


Figure 5: Dung beetle abundance in three different — and the forest matrix surrounding patches.

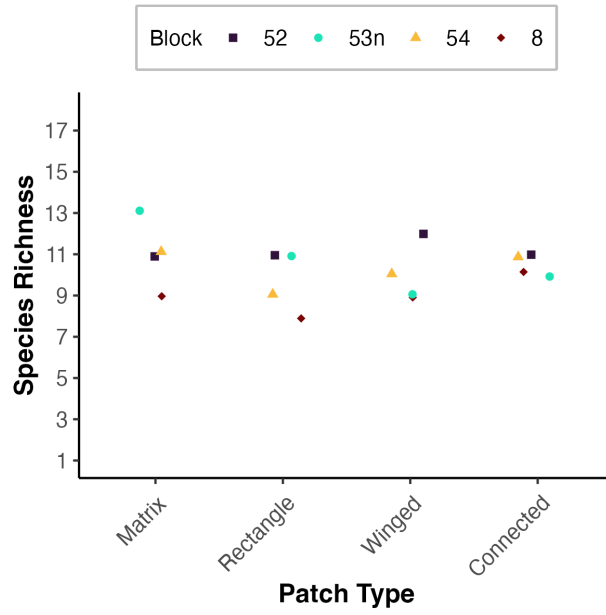


Figure 6: Dung beetle species richness in three different — and the forest matrix surrounding patches.

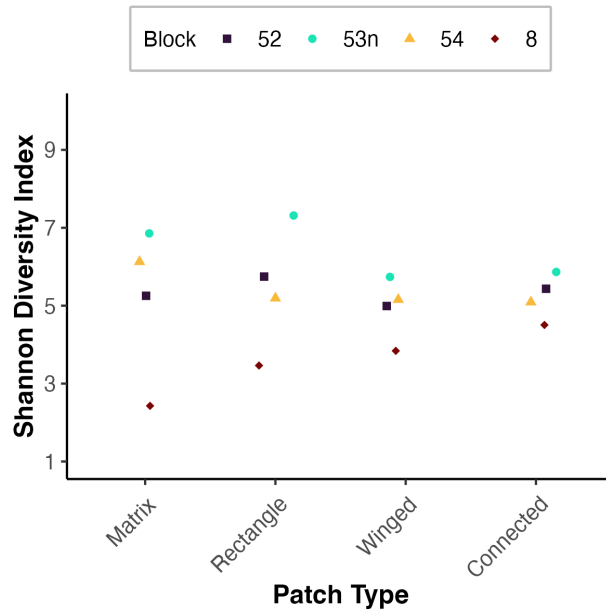


Figure 7: Dung beetle Shannon diversity in three different — and the forest matrix surrounding patches.

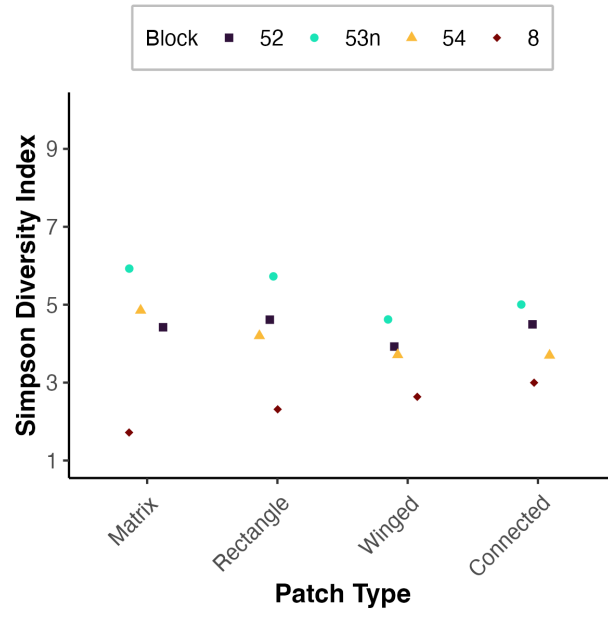


Figure 8: Dung beetle Simpson's index in three different — and the forest matrix surrounding patches.

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>	dwel	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>	dwel	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: Bray-Curtis dissimilarity comparing composition of dung beetles between patches.

Corridor	Matrix	Rectangle	Winged
0.000	0.127	0.217	0.077
0.127	0.000	0.318	0.189
0.217	0.318	0.000	0.156
0.077	0.189	0.156	0.000

Table 4: AOV TABLE CAPTION

effect	group	term	estimate	std.error	statistic	p.value
fixed		(Intercept)	3.124	0.294	10.629	0.000
fixed		patch_typeConnected	-0.125	0.139	-0.901	0.368
fixed		patch_typeRectangle	-0.528	0.107	-4.921	0.000
fixed		patch_typeWinged	-0.303	0.072	-4.189	0.000
ran_pars	block	sd__(Intercept)	0.585	NA	NA	NA
ran_pars	block	cor__(Intercept).patch_typeConnected	-0.932	NA	NA	NA
ran_pars	block	cor__(Intercept).patch_typeRectangle	-0.744	NA	NA	NA
ran_pars	block	cor__(Intercept).patch_typeWinged	-0.967	NA	NA	NA
ran_pars	block	sd__patch_typeConnected	0.266	NA	NA	NA
ran_pars	block	cor__patch_typeConnected.patch_typeRectangle	0.865	NA	NA	NA
ran_pars	block	cor__patch_typeConnected.patch_typeWinged	0.816	NA	NA	NA
ran_pars	block	sd__patch_typeRectangle	0.194	NA	NA	NA
ran_pars	block	cor__patch_typeRectangle.patch_typeWinged	0.653	NA	NA	NA
ran_pars	block	sd__patch_typeWinged	0.117	NA	NA	NA

Table 5: aovM3 patch type effects on...

term	statistic	df	p.value
Species	1044.680	5	0
Patch type	254.638	3	0
Species x Patch type	110.372	15	0

Table 6: M3 patch type effects on...

effect	group	term	estimate	std.error	statistic	p.value
fixed		(Intercept)	4.170	0.261	15.948	0.000
fixed		sp_codealec	0.234	0.078	2.989	0.003
fixed		sp_codecvig	0.457	0.075	6.107	0.000
fixed		sp_codedcar	-0.518	0.096	-5.407	0.000
fixed		sp_codeopen	-1.373	0.130	-10.549	0.000
fixed		sp_codepign	-0.105	0.085	-1.231	0.218
fixed		patch_typeConnected	-0.749	0.103	-7.257	0.000
fixed		patch_typeRectangle	-1.487	0.136	-10.913	0.000
fixed		patch_typeWinged	-1.188	0.121	-9.815	0.000
fixed		sp_codealec:patch_typeConnected	0.495	0.130	3.809	0.000
fixed		sp_codecvig:patch_typeConnected	0.595	0.124	4.800	0.000
fixed		sp_codedcar:patch_typeConnected	0.567	0.153	3.715	0.000
fixed		sp_codeopen:patch_typeConnected	0.573	0.201	2.852	0.004
fixed		sp_codepign:patch_typeConnected	0.761	0.135	5.636	0.000
fixed		sp_codealec:patch_typeRectangle	0.899	0.162	5.561	0.000
fixed		sp_codecvig:patch_typeRectangle	0.834	0.158	5.287	0.000
fixed		sp_codedcar:patch_typeRectangle	0.828	0.188	4.399	0.000
fixed		sp_codeopen:patch_typeRectangle	0.794	0.243	3.266	0.001
fixed		sp_codepign:patch_typeRectangle	1.228	0.165	7.434	0.000
fixed		sp_codealec:patch_typeWinged	0.819	0.146	5.611	0.000
fixed		sp_codecvig:patch_typeWinged	0.987	0.140	7.072	0.000
fixed		sp_codedcar:patch_typeWinged	1.020	0.165	6.182	0.000
fixed		sp_codeopen:patch_typeWinged	0.410	0.240	1.711	0.087
fixed		sp_codepign:patch_typeWinged	1.037	0.151	6.853	0.000
ran_pars	block	sd__(Intercept)	0.509	NA	NA	NA

Table 7: Richness Model

effect	term	estimate	std.error	statistic	p.value
fixed	(Intercept)	2.351	0.154	15.239	0.000
fixed	Patch Type: Matrix	0.047	0.216	0.216	0.829
fixed	Patch Type: Rectangle	-0.074	0.222	-0.333	0.739
fixed	Patch Type: Winged	-0.049	0.221	-0.221	0.825

Table 8: Shannon Diversity Model

effect	group	term	estimate	std.error	statistic
fixed		(Intercept)	5.287	0.665	7.952
fixed		patch_typeMatrix	-0.085	0.495	-0.171
fixed		patch_typeRectangle	0.149	0.495	0.301
fixed		patch_typeWinged	-0.335	0.495	-0.677
ran_pars	block	sd__(Intercept)	1.130	NA	NA
ran_pars	Residual	sd__Observation	0.701	NA	NA

Table 9: Simpson's Index Model

effect	group	term	estimate	std.error	statistic
fixed		(Intercept)	4.074	0.640	6.368
fixed		patch_typeMatrix	0.107	0.411	0.259
fixed		patch_typeRectangle	0.165	0.411	0.402
fixed		patch_typeWinged	-0.373	0.411	-0.909
ran_pars	block	sd__(Intercept)	1.140	NA	NA
ran_pars	Residual	sd__Observation	0.581	NA	NA

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 leads 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.

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.

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).
[EB edit: these last sentences don't really make the case for experiments, which were the initial emphasis of the paragraph. Might want to opt for another option, like the ones in the green notes below]