

THE INFLUENCE OF CONNECTIVITY ON DUNG BEETLE COMMUNITIES

By

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

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LIST OF ABBREVIATIONS

SRS: Savannah River Site.

GLMM: Generalized Linear Mixed Model.

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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 I sampled dung beetles in a landscape scale experiment. I 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

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 (Harrison and Bruna 1999, 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).

By measuring changes in biodiversity and species richness within experimental designs I am 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) Yet very few have directly compared matrix and patch populations. 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 (Haddad 1999).

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. 2016b). 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, I 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. I 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). I do so I address these questions:

- (1) How does the abundance of dung beetles differ among and between isolated and

- connected patches and how does this compare with abundance in matrix habitat?
- (2) Does species richness and diversity differ between among connected patches, unconnected patches, and the matrix habitat?
 - (3) What are the implications of changes in community composition for ecosystem services and function?

Methods

Study site

My 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

Dung beetles were sampled in July and August 2024 in four of the SRS blocks (8, 52, 53n, and 54; Figure 1). In each block sampling was conducted using baited pitfall traps placed in each patch type as well as the matrix surrounding the patches (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. I 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 using 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 upon completion of all analyses.

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). I 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 I compared the values of the Hill Shannon and Simpson indexes in the different patch types and matrix. For abundance and richness I 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. I included the identity of the sampling block as a random effects. To model my diversity metrics I 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 my modeling I evaluated the the suitability of my data with *qqplots* generated with the `DARMA` package (Hartig 2024).

I 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 ($N = 1359$ in Connected patches, $N = 1199$ in Winged patches, $N = 942$ in Rectangle patches, $N = 1713$ in the Matrix). These beetles belonged 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 overall abundance of beetles (all species combined) across patch types, matrix plots had the highest captures, followed by connected patches, then winged, with the fewest in rectangular patches. Abundances from connected patches were not significantly different from those in the matrix while rectangle and winged patches had significantly fewer than the matrix ($\beta = -0.528$ and -0.303 respectively, $P < 0.001$, 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 matrix patches. Compared to this baseline, results were highly variable, emphasizing species specific responses to patch type. Similarly, species showed to have disproportionate responses to patch since interaction terms varied widely (Table 6).

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 matrix patches as a baseline resulted in no significant differences in connected ($\beta = 0.216$, $p = 0.839$; Table 7), rectangle ($\beta = -0.548$, $p = 0.583$; Table 7), and winged patches ($\beta = -0.095$, $p = 0.663$; Table 7).

Biodiversity was also even among patch types, however metric values were varied by sampling blocks. For Shannon Diversity, the estimated mean in matrix patches was 5.202 (SE = 0.665, $t = 7.825$). None of the alternative patch types showed statistically significant differences compared to matrix: connected ($\beta = -0.085$, SE = 0.495, $t = 0.17$), rectangle ($\beta = 0.234$, SE = 0.495, $t = 0.472$), or winged ($\beta = -0.251$, SE = 0.495, $t = -0.506$). Similarly, for Simpson's Diversity, the average value in matrix patches was 4.181 (SE = 0.640, $t = 6.535$). Again, none of the other patch types had significant effects: matrix ($\beta = -0.107$, SE = 0.411, $t = -0.259$), rectangle ($\beta = 0.059$, SE = 0.411, $t = 0.143$), and winged ($\beta = -0.480$, SE = 0.411, $t = -1.169$).

Discussion

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. My main findings emphasized: (1) Habitat type and patch shape were the main driving factors for determining how 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.

In my comparison of dung beetle compositions, connectivity and habitat edge accounted for differences in dung beetle abundances, yet species richness and diversity were even across patch types and in the matrix. Total beetle counts were consistently highest in the matrix, in comparison abundances in connected patches were not significantly different while those of the winged and rectangular patches were lower. Additionally, I also observed that patch effects were not equally proportional for all species. This suggests that the species captured could be exhibiting habitat preferences between the open patches versus forested matrix. Another potential explanation is that species in the matrix are acting as a source population which feeds into patches with edge acting as a drift fence for directing movement. The latter example seems more likely because flies, which have similar resource dependencies were also found to have a similar interaction (Fried et al. 2005), and also studies on dung beetles in the tropics found more dramatic differences in dung beetle populations in fragments and matrix (Barragan et al. 2011).

Although richness and diversity were the same among treatments, there was notable variability between sampling blocks. Block 8 generally had the lowest species richness and biodiversity while 53n had the highest. While the design of the experimental blocks control for as much as possible, landscape features across the site are different enough to influence species composition. Several factors may explain this pattern, at the time this study was conducted block 8 had the densest matrix of any of the other sampling blocks which could have hindered the scent permeability of the bait. Other habitat characteristics might have been influential as well, including soil quality and forest cover which can determine where

beetles can reproduce (Arellano et al. 2008, Conover et al. 2019) Not only do these impact dung beetle movement, but also these landscape features can affect mammal movement, which in turn limits dung availability for beetles. In this regard it is also important to consider other geographical differences, block 8 was nearest to roadways used by all employees at SRS and the eastern side of the sight had large bodies of water. Both of which would effect the land-use by larger mammals (Harvey et al. 2006, Dechen Quinn et al. 2013, Barahona-Segovia 2021). Additionally, deer and feral hogs are the most dominant mammals at the site, two species that do well in patchy landscapes (Castillo-Contreras et al. 2018, Fraser et al. 2019). This might explain the lack of variation in richness or diversity in patches while differences are more apparent at greater distances across the site.

Species specific differences are apparent but do not follow any particular trend. *Aphodius alloblackburneius* had a disproportionate positive effect to being captured in matrix patches as compared to other species. Beetles from the genus *Aphodius* do tend to show patterns of habitat specificity (Roslin and Koivunen 2001), and many preferring forested habitat, so it is not unexpected that they might show a preference towards forested matrix. I did not detect that any species was more positively associated with open patches despite expectations that some species (e.g., *Canthon vigilans*, *Melanocanthon bispinatus*) would prefer open habitat (Nealis 1977, Conover et al. 2019). Altogether this could be another sign pointing towards matrix acting as a source population, and since open habitat was much less dominant in my experimental system beetles could be moving into patches from habitat edge.

Despite ample work documenting their ecological importance, there is a surprising lack of research on dung beetle diversity and corridors outside of the tropics (Nichols et al. 2007), with any work in temperate locations coming from Europe where *Aphodius* beetles dominate (Roslin and Koivunen 2001). Many studies in the tropics have found patterns of habitat preference between open fields and continuous forest similar to what I did in this study (Damborsky et al. 2015), and some work that found that forest species were using living

fences as corridors (Arellano et al. 2008). However, differences in composition were much more distinctly different with some species being exclusive to habitat types unlike I see in this paper. Of the limited work out of the south eastern United States I did recover assemblages similar to other work (Nealis 1977, Conover et al. 2019), and even returned results to another study where differences between treatment types were non-significant while variation on a larger scale was more apparent (Young et al. 2023). In comparison to other studies from SRS my results were similar to those of small mammals which were more likely to be using matrix land (Mabry et al. 2003). I did expect some species to be more dominant in patches with higher edge ratios as was found with ants at SRS (Resasco et al. 2014), but species were evenly present in all patches.

There were some limitations of this study which should be addressed in any future work to capture a clearer picture of how populations are being altered by habitat connectivity. First, sampling for this study was conducted over a two month period in the summer of 2024, sufficient data was collected but due to a lack of available resources temporal patterns were obscured due to inconsistent sampling periods. This is highly important since dung beetles exhibit consistent patterns of seasonality (Davis 1966, Conover et al. 2019). Another potential avenue for improvement is lowering the grain size of sampling and changing trap placement to better understand the effects of edge proximity and connectivity. I also used one of the best bait types for collecting dung beetles in pig dung (Marsh et al. 2013), but a mix of differently sourced baits may have been more optimal as more diverse baits attract more diverse species (Frank et al. 2017, 2018, Giménez Gómez et al. 2021).

Moving forward, there is a bounty of knowledge yet to be collected for dung beetles in the south eastern United States. Relative to what is already known in tropical ecosystems, this study provides a glimpse on how dung beetles are responding to fragmentation and connectivity in subtropic pine habitats, but much can still be learned about dung beetles in these spaces and the role they play in ecosystems as well as how they interact with

landscapes. The unique role of dung beetles as waste removers is fascinating enough and of great importance for maintaining landscapes so dominated by pastures like Southern US (Slade et al. 2016a, Cheng et al. 2022). Not only waste removal but also secondary effect such as seed dispersal and parasitic reduction are important to understand in the context of fragmentation (Fincher 1975, Vulinec 2002). SRS provides an excellent experimental design for direct comparison of landscapes but another main goal of the site is to study dispersal, dung beetles would be an excellent system for studying movement. They already show promise, in preliminary trials I released beetles from both the connected and rectangular patches with baited traps in the central patch. I recovered one recapture which originated from the connected patch, indicating that individuals do move through corridors.

Although there is plentiful work to be done, this study paints an encouraging picture that while dung beetles face disturbances that make habitats less preferential, they are robust enough to persist throughout fragmented landscapes and the management strategies we do have to connect fragmented landscapes work to mitigate losses. Because assemblages remain mostly the same across these landscapes, ecosystem services should remain uninterrupted allowing continuing benefits to all community members. While this study of dung beetles in fragmented landscapes was conducted in a relatively protected area, in real world application we could consider the use of movement corridors within disturbed areas to help bolster effected populations, but also near areas of high importance such as pastures to provide areas of refuge for beetles. In this case it is important to consider the inverse of what was manipulated in this study where open field acts as matrix and forested area is focal landscape, thus it is vital to continue learning more about how landscape composition and connectivity effect dung beetle populations.

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.
- Barahona-Segovia, R. M. 2021. Until death do us part: Abundance and survival of necrophagous beetle species associated with fox scats in fragmented landscapes. *Journal of Insect Conservation* 25:521–530.
- Barragan, F., C. E. Moreno, F. Escobar, G. Halffter, and D. Navarrete. 2011. Negative impacts of human land use on dung beetle functional diversity. *Plos One* 6.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67:1–48.
- 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.
- Castillo-Contreras, R., J. Carvalho, E. Serrano, G. Mentaberre, X. Fernández-Aguilar, A. Colom, C. González-Crespo, S. Lavín, and J. R. López-Olvera. 2018. Urban wild boars prefer fragmented areas with food resources near natural corridors. *Science of The Total Environment* 615:282–288.
- 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.
- Cheng, J., F. Y. Li, Y. Wang, Y. Wang, X. Liu, J. Zhang, Z. Wang, Y. Li, H. Wang, Z. Yang, and M. A. Potter. 2022. Dweller and tunneler dung beetles synergistically accelerate decomposition of cattle and horse dung in a semi-arid steppe. *Agriculture, Ecosystems & Environment* 329:107873.
- 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.
- Damborsky, M. P., M. C. Alvarez Bohle, M. G. Ibarra Polesel, E. A. Porcel, and J. L. Fontana. 2015. Spatial and temporal variation of dung beetle assemblages in a fragmented landscape at eastern humid chaco. *Neotropical Entomology* 44:30–39.
- Davis, L. V. 1966. Feeding habits and seasonal distribution of scarab beetles in the North Carolina piedmont. *Journal of the Elisha Mitchell Scientific Society* 82:212–220.
- 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.
- Dechen Quinn, A. C., D. M. Williams, and W. F. Porter. 2013. Landscape structure influences space use by white-tailed deer. *Journal of Mammalogy* 94:398–407.
- 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: Deltochilini). *Insecta Mundi*.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515.
- Fincher, G. T. 1975. Effects of dung beetle activity on the number of nematode parasites acquired by grazing cattle. *The Journal of Parasitology* 61:759.
- 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. Tschardt, 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.
- Frank, K., A. Brückner, N. Blüthgen, and T. Schmitt. 2018. In search of cues: Dung beetle attraction and the significance of volatile composition of dung. *Chemoecology* 28:145–152.
- Frank, K., A. Brückner, A. Hilpert, M. Heethoff, and N. Blüthgen. 2017. Nutrient quality of vertebrate dung as a diet for dung beetles. *Scientific Reports* 7:12141.
- Fraser, D. L., K. Ironside, R. K. Wayne, and E. E. Boydston. 2019. Connectivity of mule deer (*Odocoileus hemionus*) populations in a highly fragmented urban landscape. *Landscape Ecology* 34:1097–1115.
- Fried, J. H., D. J. Levey, and J. A. Hogsette. 2005. Habitat corridors function as both drift fences and movement conduits for dispersing flies. *Oecologia* 143:645–651.
- Giménez Gómez, V. C., J. R. Verdú, S. J. E. Velazco, and G. A. Zurita. 2021. Dung beetle

- trophic ecology: Are we misunderstanding resources attraction? *Ecological Entomology* 46:552–561.
- 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. 1999. Corridor use predicted from behaviors at habitat boundaries. *The American Naturalist* 153:215–227.
- 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.
- Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: What do we know for sure? *Ecography* 22:225–232.
- Hartig, F. 2024. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.
- Harvey, C. A., A. Medina, D. Merlo Sanchez, S. Vilchez, B. Hernandez, J. C. Saenz, J. M. Maes, F. Casanoves, and F. L. Sinclair. 2006. Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecological Applications* 16:1986–1999.
- 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.
- 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.
- Mabry, K. E., E. A. Dreelin, and G. W. Barrett. 2003. Influence of landscape elements on population densities and habitat use of three small-mammal species. *Journal of Mammalogy* 84:20–25.
- Marsh, C. J., J. Louzada, W. Beiroz, and R. M. Ewers. 2013. Optimising bait for pitfall trapping of Amazonian dung beetles (Coleoptera: Scarabaeinae). *Plos One* 8:e73147.
- 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., T. Larsen, S. Spector, A. L. Davis, F. Escobar, M. Favila, K. Vuline, and S. R. Network. 2007. Global dung beetle response to tropical forest modification and

- fragmentation: A quantitative literature review and meta-analysis. *Biological Conservation* 137:1–19.
- 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.
- Resasco, J., N. M. Haddad, J. L. Orrock, D. Shoemaker, L. A. Brudvig, E. I. Damschen, J. J. Tewksbury, and D. J. Levey. 2014. Landscape corridors can increase invasion by an exotic species and reduce diversity of native species. *Ecology* 95:2033–2039.
- 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.
- Roslin, T., and A. Koivunen. 2001. Distribution and abundance of dung beetles in fragmented

- landscapes. *Oecologia* 127:69–77.
- Slade, E. M., T. Riutta, T. Roslin, and H. L. Tuomisto. 2016a. The role of dung beetles in reducing greenhouse gas emissions from cattle farming. *Scientific Reports* 6.
- Slade, E. M., T. Roslin, M. Santalahti, and T. Bell. 2016b. Disentangling the “brown world” faecal-detritus interaction web: Dung beetle effects on soil microbial properties. *Oikos* 125:629–635.
- 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.
- Vulinec, K. 2002. Dung beetle communities and seed dispersal in primary forest and disturbed land in amazonia. *Biotropica* 34:297–309.
- 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.
- Young, K., A. Tsalickis, T. N. Sheehan, K. D. Klepzig, M. S. Caterino, and J. A. Hartshorn. 2023. Dung beetle community composition in the presence and absence of mesopredators in a longleaf pine forest. *Southeastern Naturalist* 22:78–90.
- 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.

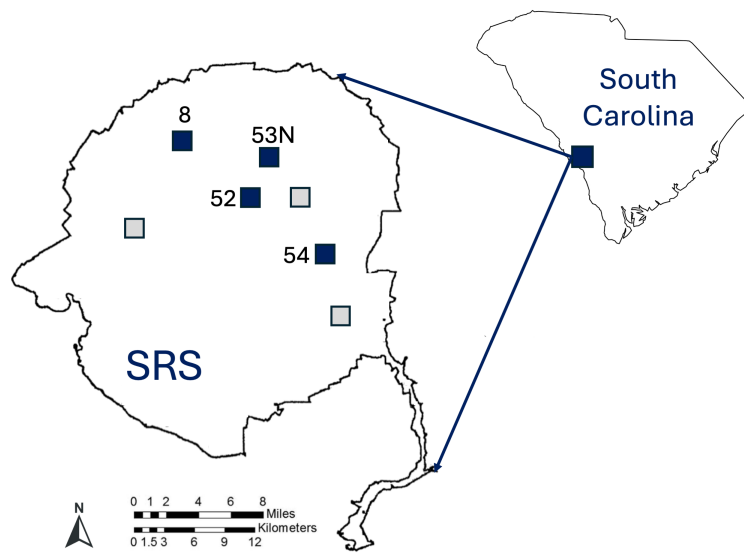


Figure 1: All experimental blocks at SRS. Filled squares indicate the blocks in which dung beetles were sampled. Each block has a unique ID number.

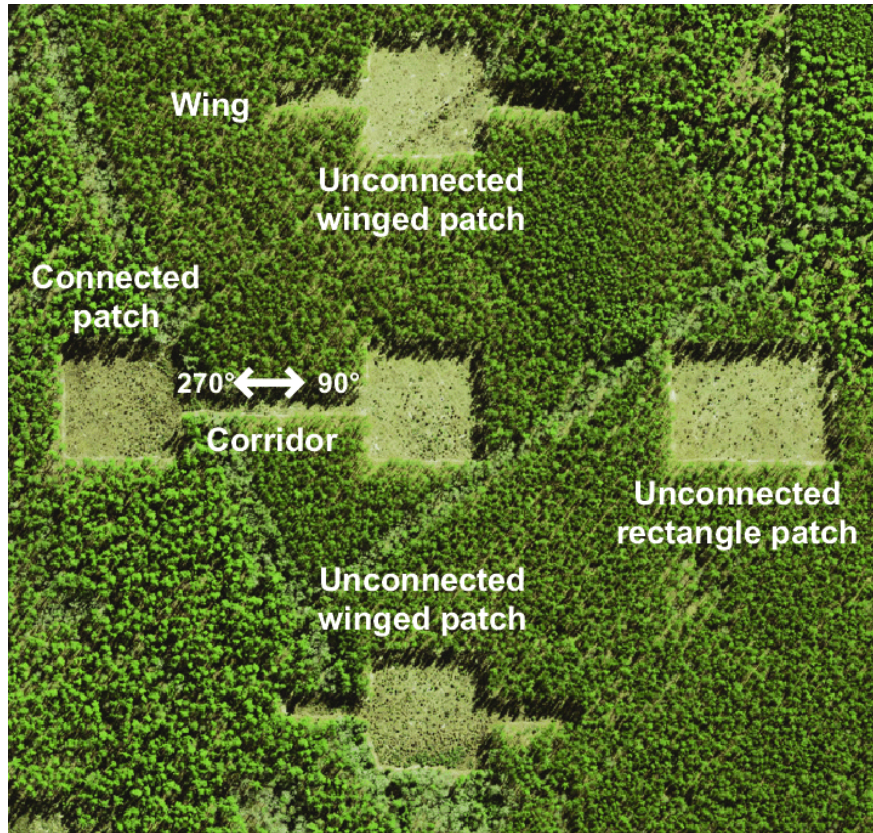


Figure 2: Overhead view of one of the experimental blocks indicating the different types of patches and the distance between them (from Nathan et al. 2018 and reused with permission).

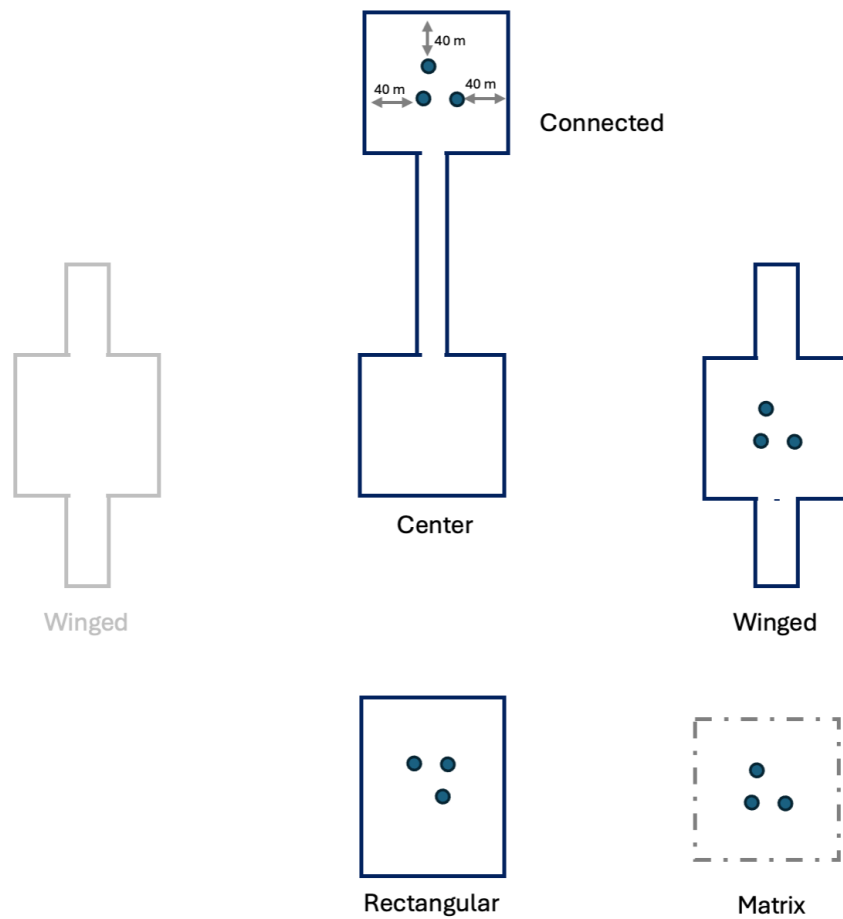


Figure 3: Diagram indicating the placement pitfall traps in each patch and in the matrix. Traps in patches were approximately 40 m from the patch edge.

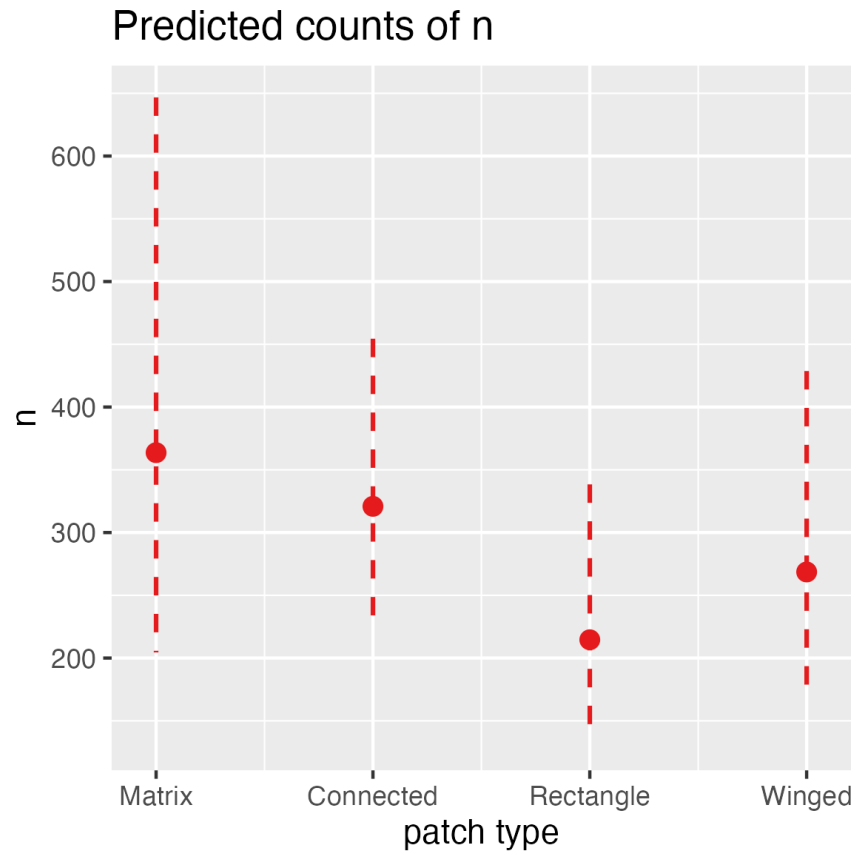


Figure 4: Average total dung beetle abundance by patch type with standard deviations as error bars.

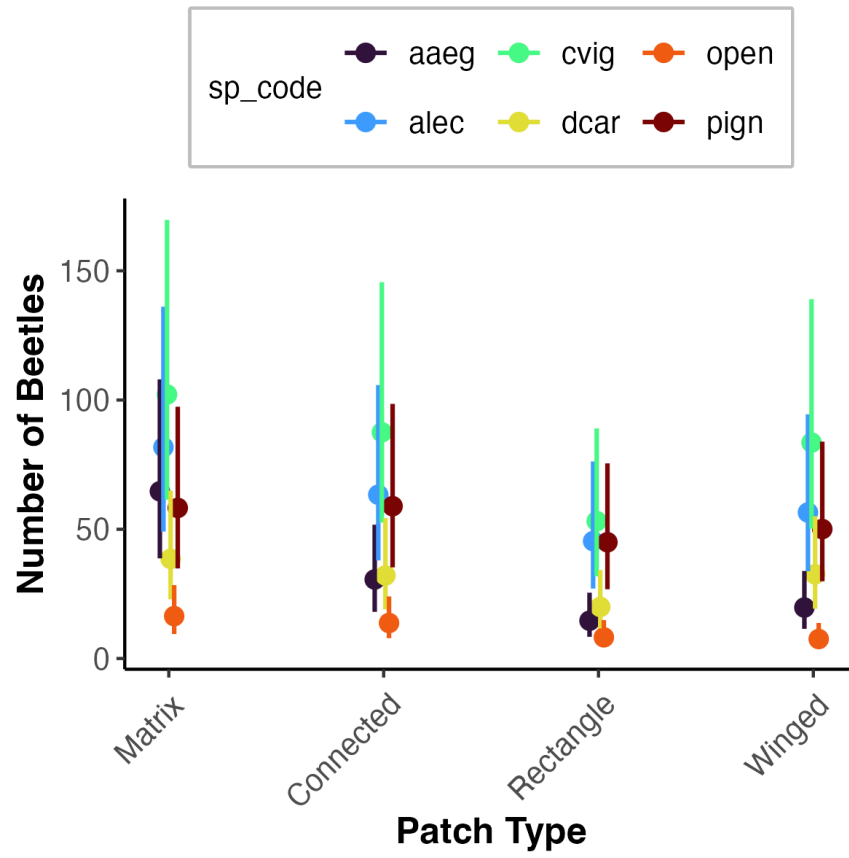


Figure 5: Average abundance of the top 6 most abundant species by patch type.

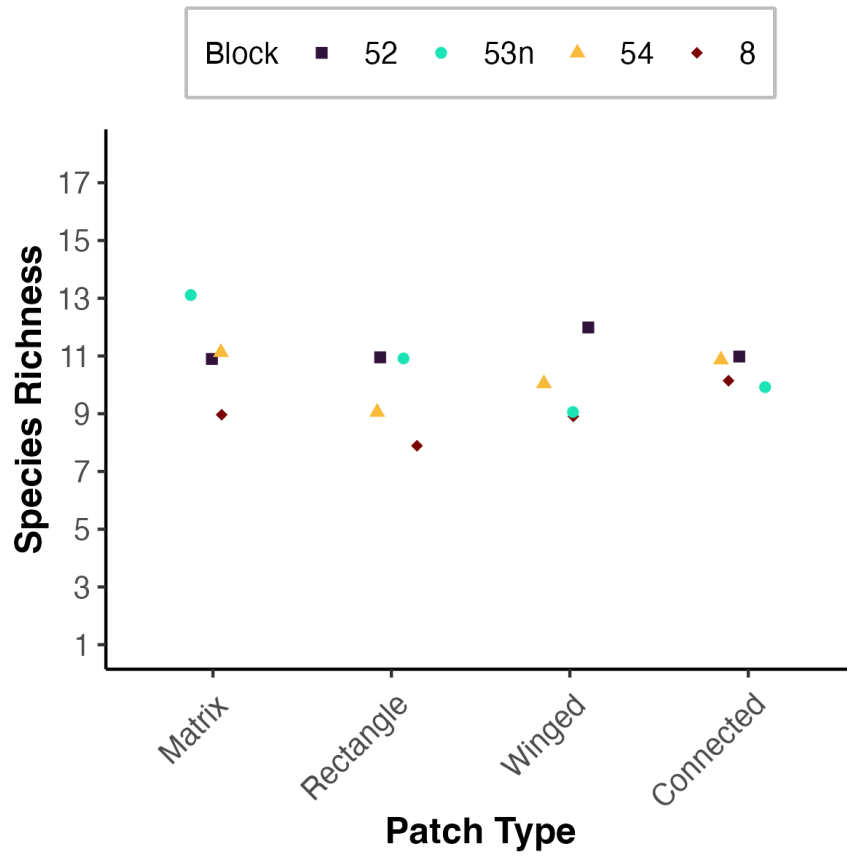


Figure 6: Dung beetle species richness in each patch type. The point shapes indicates the block in which each patch was located.

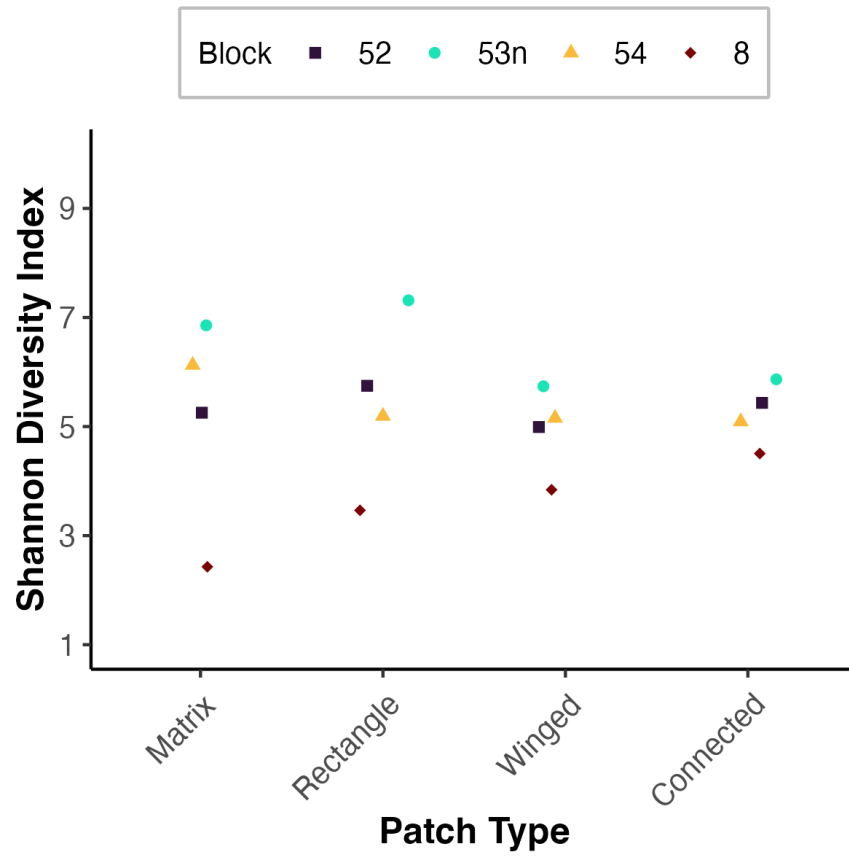


Figure 7: Dung beetle Shannon diversity by patch type.

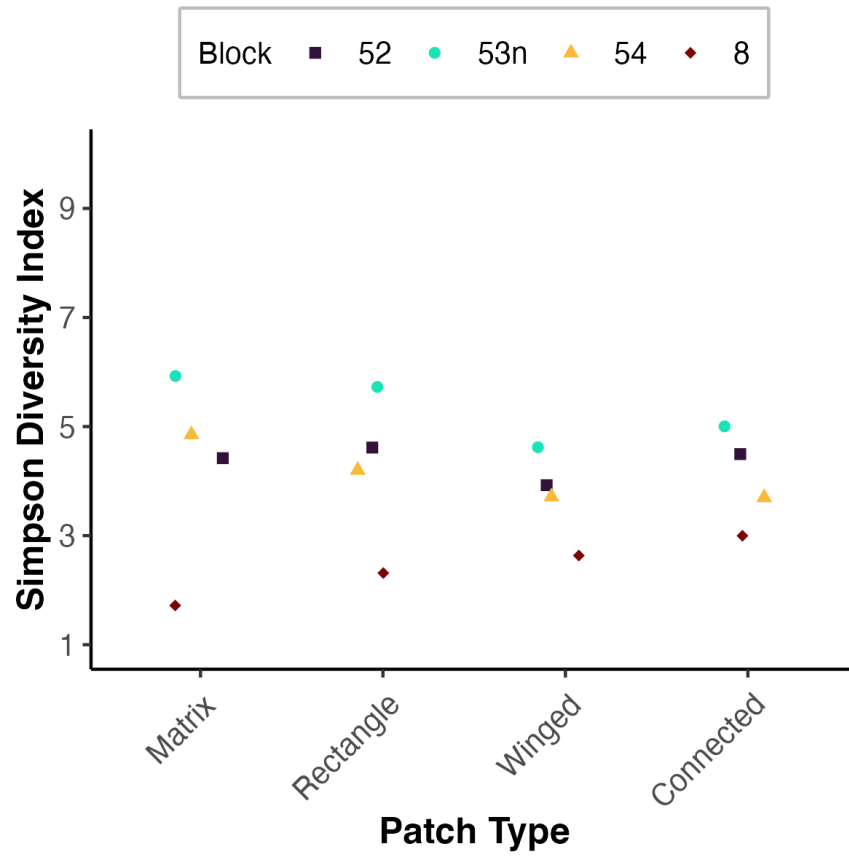


Figure 8: Dung beetle Simpson's index y patch type.

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

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

Table 3: Model of species abundance by patch type.

Effect	Group	Term	Estimate	SE	Statistic	P
Fixed		(Intercept)	5.896	0.294	20.062	< 0.001
Fixed		patch type - Connected	-0.125	0.139	-0.9	0.368
Fixed		patch type - Rectangle	-0.528	0.107	-4.919	< 0.001
Fixed		patch type - Winged	-0.303	0.072	-4.188	< 0.001
Random	Block	SD: (Intercept)	0.585			
Random	Block	correlation: (Intercept) x patch type - Connected	-0.932			
Random	Block	correlation: (Intercept) x patch type - Rectangle	-0.744			
Random	Block	correlation: (Intercept) x patch type - Winged	-0.967			
Random	Block	SD: patch type - Connected	0.266			
Random	Block	correlation: patch type - Connected x patch type - Rectangle	0.865			
Random	Block	correlation: patch type - Connected x patch type - Winged	0.816			
Random	Block	SD: patch type - Rectangle	0.194			
Random	Block	correlation: patch type - Rectangle x patch type - Winged	0.653			
Random	Block	SD: patch type - Winged	0.116			

Table 4: AOV patch type effects on species abundance and interavtive term.

Term	Statistic	df	P
Species	1044.680	5	< 0.001
Patch type	254.638	3	< 0.001
Species x Patch type	110.372	15	< 0.001

Table 5: M3 patch type effects on species abundance of top 6 most abundant speceies and interactive term for patch type and species ID.

Effect	Group	Term	Estimate	SE	Statistic	P
Fixed		(Intercept)	4.17	0.261	15.948	< 0.001
Fixed		Species - alec	0.234	0.078	2.989	0.003
Fixed		Species - cvig	0.457	0.075	6.107	< 0.001
Fixed		Species - dcar	-0.518	0.096	-5.407	< 0.001
Fixed		Species - open	-1.373	0.13	-10.549	< 0.001
Fixed		Species - pign	-0.105	0.085	-1.231	0.218
Fixed		patch type - Connected	-0.749	0.103	-7.257	< 0.001
Fixed		patch type - Rectangle	-1.487	0.136	-10.913	< 0.001
Fixed		patch type - Winged	-1.188	0.121	-9.815	< 0.001
Fixed		Species - alec : patch type - Connected	0.495	0.13	3.809	< 0.001
Fixed		Species - cvig : patch type - Connected	0.595	0.124	4.8	< 0.001
Fixed		Species - dcar : patch type - Connected	0.567	0.153	3.715	< 0.001
Fixed		Species - open : patch type - Connected	0.573	0.201	2.852	0.004
Fixed		Species - pign : patch type - Connected	0.761	0.135	5.636	< 0.001
Fixed		Species - alec : patch type - Rectangle	0.899	0.162	5.561	< 0.001
Fixed		Species - cvig : patch type - Rectangle	0.834	0.158	5.287	< 0.001
Fixed		Species - dcar : patch type - Rectangle	0.828	0.188	4.399	< 0.001
Fixed		Species - open : patch type - Rectangle	0.794	0.243	3.266	0.001
Fixed		Species - pign : patch type - Rectangle	1.228	0.165	7.434	< 0.001
Fixed		Species - alec : patch type - Winged	0.819	0.146	5.611	< 0.001
Fixed		Species - cvig : patch type - Winged	0.987	0.14	7.072	< 0.001
Fixed		Species - dcar : patch type - Winged	1.02	0.165	6.182	< 0.001
Fixed		Species - open : patch type - Winged	0.41	0.24	1.711	0.087
Fixed		Species - pign : patch type - Winged	1.037	0.151	6.853	< 0.001
Random	Block	SD : (Intercept)	0.509			

Table 6: Richness Model

Effect	Term	Estimate	SE	Statistic	P
Fixed	(Intercept)	2.398	0.151	15.906	< 0.001
Fixed	Patch Type - Connected	-0.047	0.216	-0.216	0.829
Fixed	Patch Type - Rectangle	-0.121	0.22	-0.548	0.583
Fixed	Patch Type - Winged	-0.095	0.218	-0.436	0.663

Table 7: Shannon Diversity Model

Effect	Group	Term	Estimate	SE	Statistic
Fixed		(Intercept)	5.202	0.665	7.825
Fixed		patch type - Connected	0.085	0.495	0.171
Fixed		patch type - Rectangle	0.234	0.495	0.472
Fixed		patch type - Winged	-0.251	0.495	-0.506
Random	Block	SD: (Intercept)	1.13		
Random	Residual	SD: Observation	0.701		

Table 8: Simpson's Index Model

Effect	Group	Term	Estimate	SE	Statistic
Fixed		(Intercept)	4.181	0.64	6.535
Fixed		patch type - Connected	-0.107	0.411	-0.259
Fixed		patch type - Rectangle	0.059	0.411	0.143
Fixed		patch type - Winged	-0.48	0.411	-1.169
Random	Block	SD: (Intercept)	1.14		
Random	Residual	SD: Observation	0.581		

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.