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

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

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ABBREVIATIONS

GLMM   Generalized Linear Mixed Model.

SRS   Savannah River Site

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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 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 corridor than in isolated patches.

CHAPTER 1
INTRODUCTORY REMARKS

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).

CHAPTER 2
STUDY DESIGN, RESTULTS, AND DISCUSSION

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 that 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). 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

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 and weighed for biomass measurements. Ten species had the required

counts for weighing which I dried in drying oven until all specimen reached a stable

mass. I weighed each beetle using an Ohaus Adventurer Pro AV53 microbalance, with

the exception of individuals whose weights were extremely small. Individual biomass for

these species was estimated by weighing in batches of N = 3 (i.e., *Ateuchus lecontei*), N

= 5 (i.e., *Onthophagus pennsylvanicus*), or N = 15 (i.e., *Aphodius alloblackburneus*) and

then calculated by average biomass per beetle. Values for individual biomass were then

used to estimate the total biomass of each species in each patch, as well as the total

beetle biomass (i.e., all species combined) in each patch. 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). 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 effect. 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 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. Likewise, I used linear mixed-effects models to compare for differences between patch types in (1) total dung beetle biomass, and (2) the total biomass of each of the ten species, again including block as a random effect.

Results

Beetle Abundance

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: (N = 1473), (N = 1115), (N = 958), (N = 585), (N = 556), and (N = 207; Table 1). All but four species were captured in every patch type. *Onthophagus concinnus* was only found in the matrix and winged patches, while *Onthophagus striatulus* was only captured in matrix habitat and rectangular patches. *Geotrupes blackburnii* and *Onthophagus tuberculifrons* were the only species restricted to one patch type (winged and matrix, respectively). All species were within their native ranges.

When comparing the 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 (Figure 4). Abundances from connected patches were not significantly different from those in the matrix while rectangle and winged patches had significantly fewer than the matrix (β = -0.528 and -0.303 respectively, P < 0.001, Table 2).

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 3). 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 3).

Beetle Richness and Diversity

Plotting species richness by patch type reveals consistent richness across patch types with some variation between sampling blocks (Figure 6).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 (β = 0.216, p = 0.839; Table 4), rectangle (β = -0.548, p = 0.583; Table 4), and winged patches (β = -0.095, p = 0.663; Table 4).

Biodiversity was also even not significantly different between patch types, however the values of the different metrics varied significantly across sampling blocks (Figures 7-8). For Shannon Diversity, the estimated mean in matrix patches was 5.202 (SE = 0.665, t = 7.825; Table 5). None of the alternative patch types showed statistically significant differences compared to matrix: connected (β = –0.085, SE = 0.495, t = 0.17), rectangle (β = 0.234, SE = 0.495, t = 0.472), or winged (β = –0.251, SE = 0.495, t = –0.506; Table 5). Results for Simpson's Diversity were similar (Table 6), with the average value in matrix patches was 4.181 (SE = 0.640, t = 6.535). Again, none of the other patch types were significantly different from the others: matrix (β = -0.107, SE =

0.411, t = -0.259), rectangle (β = 0.059, SE = 0.411, t = 0.143), and winged (β = –0.480, SE = 0.411, t = –1.169; Table 6).

Dung Beetle Biomass

Patterns of biomass by patch type were similar to those for abundance: biomass was highest in matrix plots, followed by connected and winged, with biomass in rectangle patches being far lower than in the other locations (Figure 8). There was no significant difference in the total beetle biomass of matrix plots when compared to connected (β = -7.337, SE = 8.659, t = -0.847; Table 10) and winged patches (β = -9.608, SE = 8.659, t = -1.11; Table 10), but biomass in rectangle patches was significantly different (β = -23.296, SE = 8.659, t = -2.69; Table 10). Block effects continue to be important for explaining high variation as the total biomass collected in block 52 was nearly quadruple that collected in Block 8 (Figure 11). Linear mixed effects models also indicate significant differences between the biomass of different species (Table 7, Figure 9). Lastly, when plotting average individual biomass against total captures a slight positive trend can be observed between individual biomass and abundance (Figure 12).

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 is 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 - small mammals at SRS, which are a potential source of dung, appear to preferentially use matrix habitat (Mabry et al. 2003) and flies, which have similar resource dependencies were also found to have a similar interaction (Fried et al. 2005). Moreover, 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 experimental design attempted to control for the effects of patch size and edge, there could be large (and potential unknown) environmental gradients across the SRS landscape that could influence the observed patterns in diversity and abundance. For instance, at the time of my study Block 8 had the densest matrix of any of the blocks. This could have hindered the diffusion of bait scent, leading to lower capture rates in this block. Other habitat characteristics that might differ among blocks could have been influential as well – for example, soil quality and forest cover can determine where beetles can reproduce (Arellano et al. 2008, Conover et al. 2019). The same is true for land-use history; much of the SES land would have previously been used for agriculture, and during development of experimental units cleared with heavy machinery might experience heavy soil compaction (Brudvig et al. 2011). Landscape features could also affect mammal movement, which might in turn limit dung availability - Block 8 was nearest to roadways used by all employees at SRS, and the eastern side of the site had large bodies of water upon which mammals are dependent (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). The locally variable patterns of abundance in the landscape of these generalist large mammals, coupled with ability to easily move through modified landscapes, might help explain the limited variation in richness or diversity within blocks (i.e., between patch types) but large block effects. Deer also commonly forage along the edges of habitat patches and forest ecotones. If they are spending more time in these locations, the higher abundance and diversity in

connected and winged patches might in part be due to 'drift-fence' effects (Fried et al.

2005).

Species-specific differences are apparent but do not follow any particular trend.

Aphodius alloblackburneus 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 (Frank et al. 2017b), 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 suggestions that some species (e.g.,

Canthon vigilans, Melanocanthon bispinatus) preferred open habitat (Nealis 1977,

Conover et al. 2019). 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.

The patterns in dung beetle biomass largely echo what we observed for

abundance. Although biomass is understood to be positively associated with dung

removal (Slade et al. 2011), dung beetle species vary greatly in terms of morphology

and functionality (Ospina-Garcés et al. 2018) so evaluating species-specific patterns is

particularly important. Because of this we can expect that the magnitude of removal

might be greater in areas of larger biomass (i.e., matrix or connected patches), however

future work should aim to directly measure this potential pattern. Indeed, comparing the

biomass of different species emphasizes the morphological variability between our

study species - some of the most common species (e.g., *Ateuchus lecontei*, *Aphodius*

allobloackburneus) contribute very little to total biomass (Figure 9). In addition to this,

dung beetles appear to be an exception to the globally and taxonomically robust rule that abundance is negatively correlated with individual biomass (White et al. 2007). More intensive sampling could determine whether this trend is truly apparent.

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 work in temperate locations coming primarily from Europe where Aphodius beetles dominate (Roslin and Koivunen 2001). Many studies conducted in the tropics found strong preference by some species for open fields vs. continuous forest (Damborsky et al. 2015), while others found that forest species were using living fences as corridors (Arellano et al. 2008). I did not observe such intense habitat specificity, which may not be especially common outside of the tropics. I found similar patterns of community composition as did the small number of prior dung beetle biodiversity surveys conducted in the southeastern United States (Nealis 1977, Conover et al. 2019), including at least one more where differences between treatment types were non-significant while variation on a larger scale was more apparent (Young et al. 2023). 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.

Finally, it is important to emphasize that while dung beetles are capable of long-distance flight and detecting dung at distances of over 50 meters (Gray et al. 2022), the results I observed are likely the result of a mismatch between the spatial scale of the experimental replicates and dung beetle movement. Put another way, some beetles were almost certainly drawn by the dung used in baits from the matrix into the plots. If

this were an overarching effect, we'd expect all plots to be similar to the matrix, or at least to each other. The fact that rectangular are have lower abundance suggests that some sort of landscape effect is apparent, likely related to habitat edge since connected and winged patches were the most similar. To remedy this issue any future work in this site should either focus solely on dung beetles with more limited dispersal ability or consider conducting mark-release-recapture experiments in an attempt to document movements within and between 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. 2017a, 2018, Giménez Gómez et al. 2021).
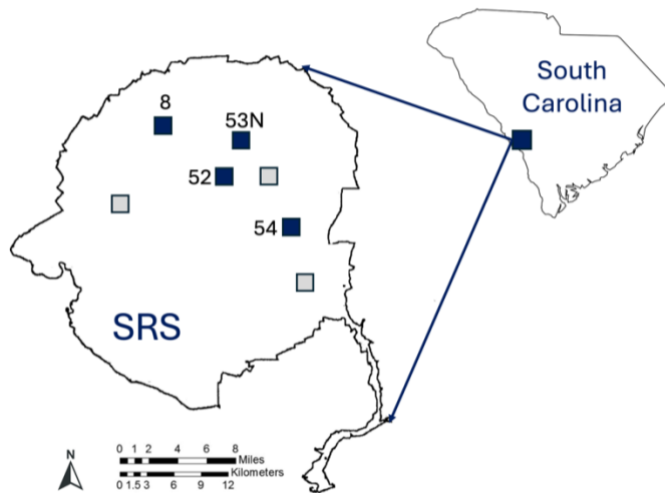
Figure 2-1. All experimental blocks at SRS. Filled squares indicate the blocks in which dung beetles were sampled. Each block has a unique ID number.
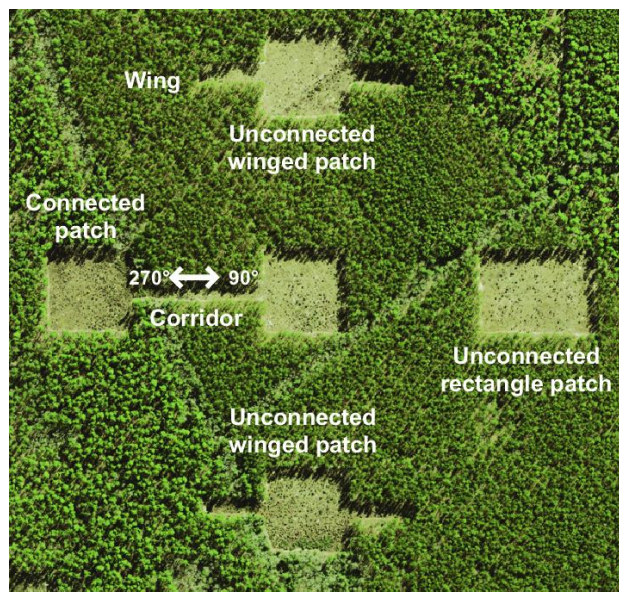
Figure 2-2. Overhead view of one of the experimental blocks indicating the different types of patches and the distance between them (from Damschen et al. 2014 and reused with permission).
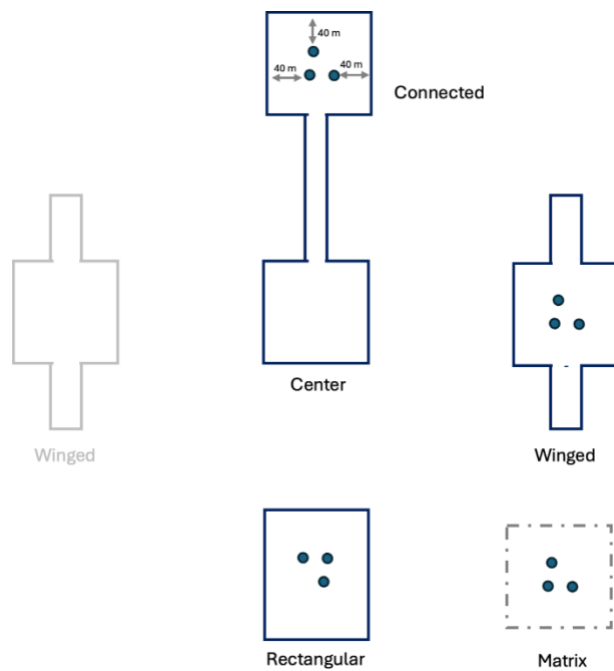
Figure 2-3. Diagram indicating the placement pitfall traps in each patch and in the matrix. Traps in patches were approximately 40 m from the patch edge.
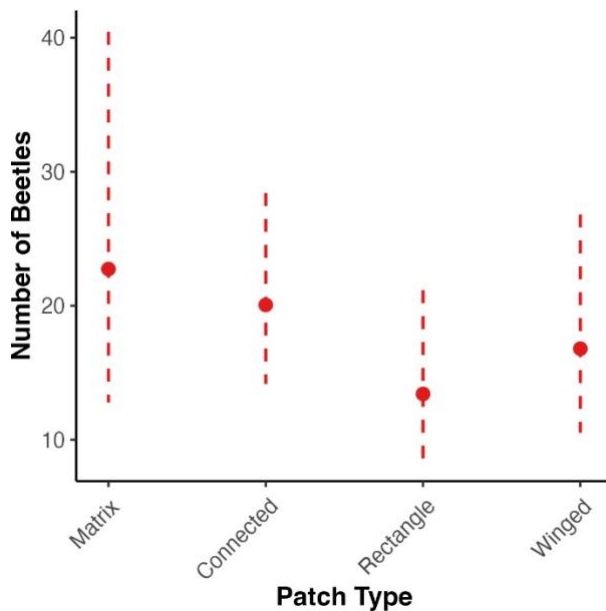
Figure 2-4. Average total dung beetle abundance by patch type with standard deviations as error bars.
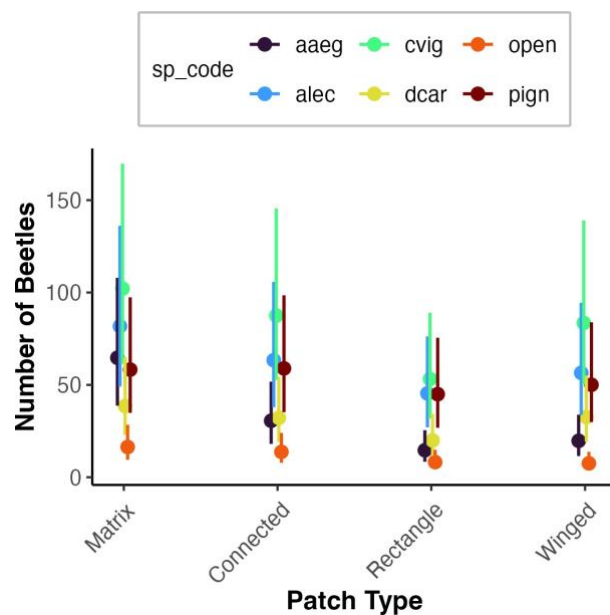
Figure 2-5. Average abundance of the top 6 most abundant species by patch type. Species codes: alec: *Ateuchus lecontei*, cvig: *Canthon vigilans*, dcar: *Dichotomius carolinus*, open: *Onthophagus pennsylvanicus*, pign: *Phanaeus igneus*, aaeg: *Aphodius alloblackburneus*.
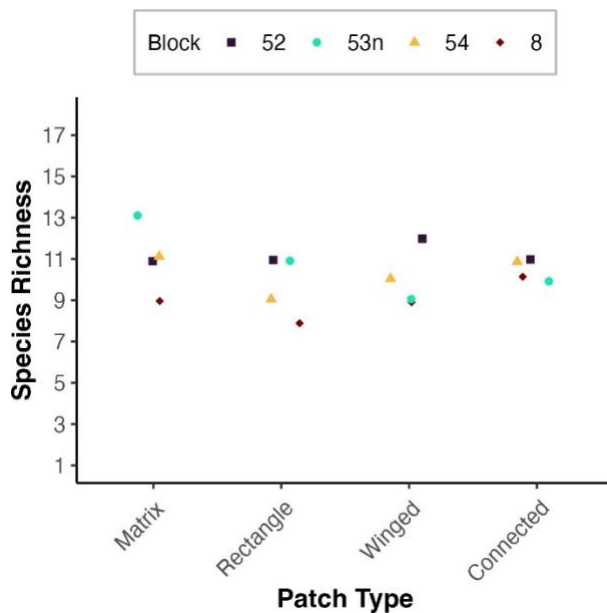
Figure 2-6. Dung beetle species richness in each patch type. The point shapes indicate the block in which each patch was located.
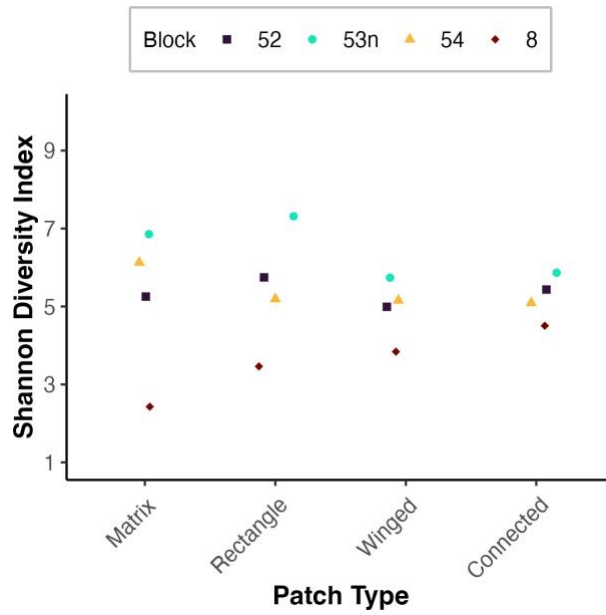
Figure 2-7. Dung beetle Shannon diversity by patch type.
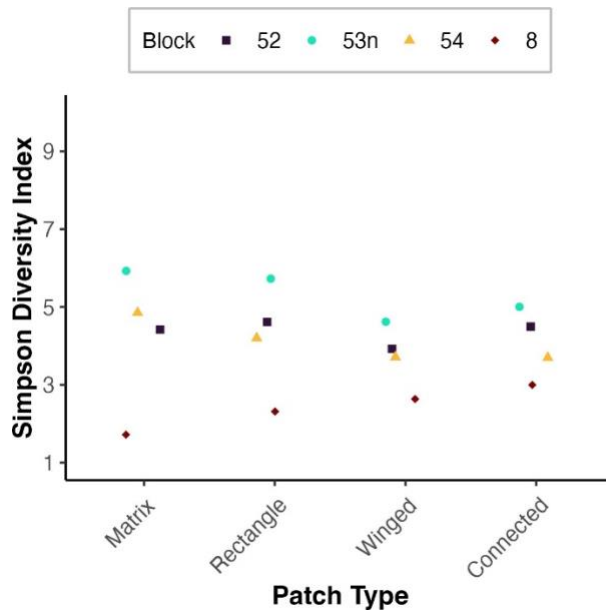
Figure 2-8. Dung beetle Simpson's index by patch type.
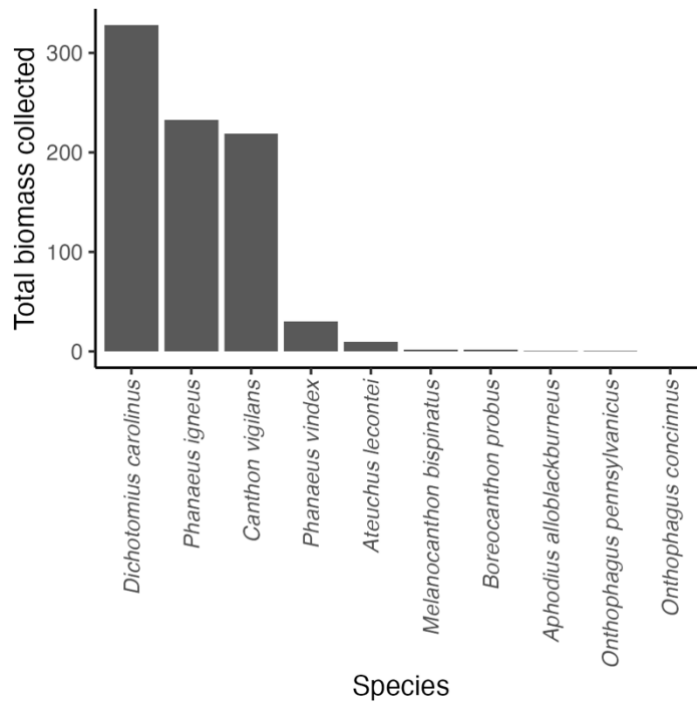
Figure 2-9. Total dung beetle biomass collected for each species with sufficient weights.
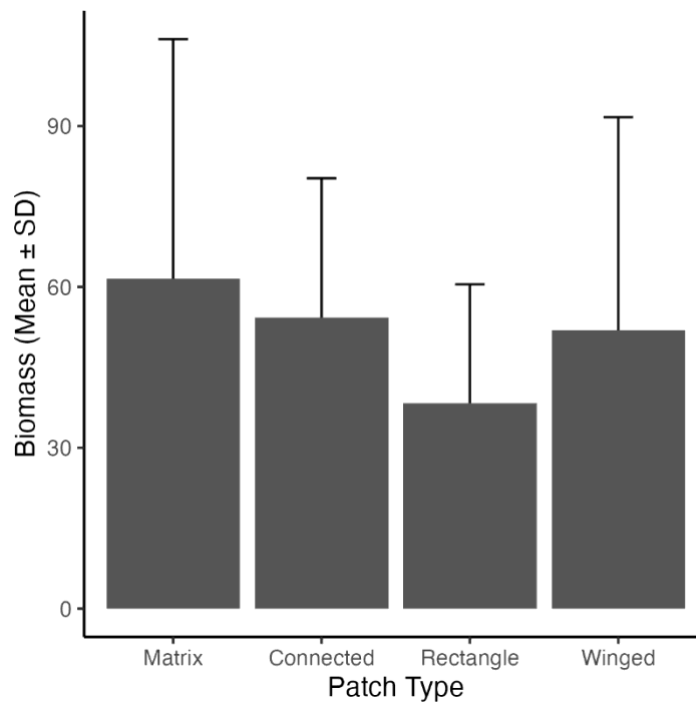
Figure 2-10. Average total biomass by patch type with standard deviation as error bars.
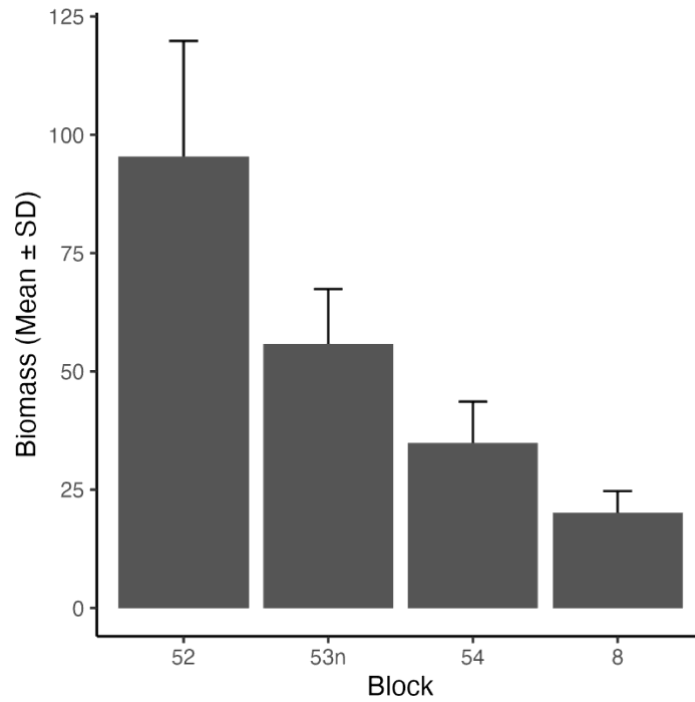
Figure 2-11. Average total biomass by sampling block with standard deviation as error bars.
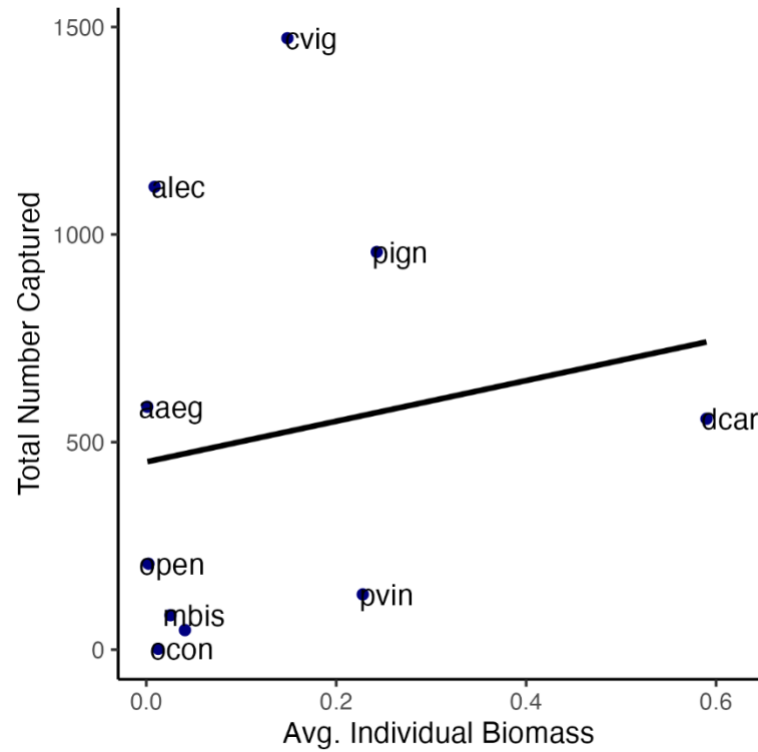
Figure 2-12. Trendline of average dung beetle biomass by total individuals captured.

Table 2-1. 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
Canthon vigilans	roll	1473	x	x	x	x
Ateuchus lecontei	tunnell	1115	x	x	x	x
Phanaeus igneus	tunnell	958	x	x	x	x
Dichotomius carolinus	tunnell	556	x	x	x	x
Aphodius alloblackburneus	dwell	585	x	x	x	x
Onthophagus pennsylvanicus	tunnell	207	x	x	x	x
Melanocanthon bispinatus	roll	83	x	x	x	x
Phanaeus vindex	tunnell	133	x	x	x	x
Boreocanthon probus	roll	47	x	x	x	x
Copris minutus	tunnell	24	x	x	x	x
Deltochilum gibbosum	roll	14	x	x	x	x
Aphodius oximus	dwell	11	x	x	x	x
Geotrupes blackburnii	tunnell	1				
Onthophagus concinnus	tunnell	2	x		x	
Onthophagus striatulus	tunnell	3	x			x
Onthophagus tuberculifrons	tunnell	1	x			

Table 2-2. 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 2-3. Generalized linear mixed model of abundance by patch type of the 6 most abundant species and interaction term forpatch type and species including sampling block as a random effect

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 2-4. Linear mixed effects model of species richness by patch type.

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 2-5. Linear mixed effects model of Shannon diversity by patch type.

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 2-6. Linear mixed effects model of Simpson's diversity by patch type.

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		

Table 2-7. Linear mixed effects model of pooled total biomass by patch type including sampling block as a random effect

Effect	Group	Term	Estimate	SE	Statistic
Fixed		(Intercept)	61.593	17.199	3.581
Fixed		Patch: Connected	-7.337	8.659	-0.847
Fixed		Patch: Rectangle	-23.296	8.659	-2.69
Fixed		Patch: Winged	-9.608	8.659	-1.11
Random	block	SD (Intercept)			
Random	Residual	SD (Observation)	12.246		

Table 2-8. Linear mixed effects model of biomass by species and patch type including sampling block as a random effect. Species codes = bpro: Boreocanthon probus, cvig: Canthon vigilans, dcar: Dichotomius carolinus, mbis: Melanocanthon bispinatus, ocon: Onthophagus concinnus, open: Onthophagus pennsylvanicus, pign: Phanaeus igneus, pvin: Phanaeus vindex

Effect	Group	Term	Estimate	SE	Statistic
Fixed		(Intercept)	1.047	2.226	0.471
Fixed		Species: alec	0.572	1.949	0.293
Fixed		Species: bpro	0.078	1.949	0.04
Fixed		Species: bvig	13.639	1.949	7
Fixed		Species: dcar	20.454	1.949	10.497
Fixed		Species: mbis	0.090	1.949	0.046
Fixed		Species: ocon	-0.040	1.949	-0.02
Fixed		Species: open	-0.012	1.949	-0.006
Fixed		Species: pign	14.484	1.949	7.433
Fixed		Species: pvin	1.853	1.949	0.951
Fixed		Patch: Connected	-0.734	1.232	-0.595
Fixed		Patch: Rectangle	-2.330	1.232	-1.89
Fixed		Patch: Winged	-0.961	1.232	-0.78
Random	block	SD (Intercept)	3.154		
Random	Residual	SD (Observation)	5.511		

CHAPTER 3
CONCLUSIONS AND FUTURE DIRECTIONS

Moving forward, there is a bounty of knowledge yet to be collected for dung beetles in the southeastern 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

36

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.

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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.