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The Structure and Assembly of Ant Communities: Patterns and Processes

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Biology

by

Douglas Brent Booher

2017

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ABSTRACT OF THE DISSERTATION

The Structure and Assembly of Ant Communities: Patterns and Processes

by

Douglas Brent Booher

Doctor of Philosophy in Biology

University of California, Los Angeles, 2017

Professor Patricia Adair Gowaty, Chair

Professor Stephen P. Hubbell, Co-Chair

Measured in species richness and abundance, ants are globally successful in temperate to tropical latitudes. Explaining the origin, success, and maintenance of diversity at both global and local scales has proven challenging because patterns of diversity and processes that drive patterns of diversity often differ between global and local scales. In this thesis, I study the patterns and processes driving ant diversity over a gradation of geographic levels. Chapter 1 compares and describes the density and dispersion of nut-nesting ants in southeastern United States temperate deciduous forests under nut producing trees. Species diversity and nut occupancy rates do not differ among sites or states and that ant-occupied nuts are spatially aggregated across ant species, a pattern inconsistent with spatial segregation of species that might arise in a competition-assembled community. In Chapter 2, through the development of new rapid sampling methods, I

determine *Strumigenys* ant communities are feasible to study. I found 0.20 ha habitats and 1.0 m^2 microsites are appropriate spatial scales for investigating abiotic factors and general habitat characteristics important for *Strumigenys* communities. I concluded that an even finer scale (< 1.0 m^2) would be necessary to investigate community patterns on spatial scales on which *Strumigenys* are likely to interact or compete.

Chapter 3 focuses on broad scale diversity patterns and describes the biogeographic origins of Nearctic *Strumigenys.* I produce a molecular based phylogeny to describe phylogenetic relationships of species and infer likely biogeographic histories of Nearctic species. I tested two alternative hypotheses for the assembly of biogeographic patterns in Nearctic *Strumigenys,* the adaptive radiation hypothesis verses the evolutionary conservatism hypothesis. Ranges of migrant or introduced species within the U.S. are consistent with average annual temperature and rainfall of ranges they occupy outside of the U.S. Results of climate and phylogenetic comparisons support predictions of the evolutionary conservatism hypothesis.

Chapter 4 examines patterns and processes in the ant genus *Strumigenys*. I examined the phylogenetic and trait relationships of co-occurring *Strumigenys* species at very small to very large geographic spatial scales to test predictions of a competition hypothesis against three alternative community assembly hypotheses. The largest geographic scale included 60,000km^2 bioregions across North America North of Mexico, to southeastern U.S. local communities of 2000m^2 and 25m^2, and 0.1m^2 microsites. Patterns of biodiversity of *Strumigenys* differed as a function of scale and suggested processes are differentially important depending on the geographic scale of pattern investigation. However, there was no evidence that competition had influenced assemblage patterns of *Strumigenys* communities at any geographic scale.

The dissertation of Douglas Brent Booher is approved.

Corrie S. Moreaux

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University of California, Los Angeles

2017

TABLE OF CONTENTS

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1. Chapter 1. Density and Dispersion of Cavity Dwelling Ant Species in Nuts of Eastern U.S. Forest Floors

1.1 ABSTRACT

Here we report on nut-nesting ant communities in the southeastern United States. We compared species diversity, ant abundance, and nut occupancy rates among sites in five states, and report the spatial dispersion of ant colonies in nuts in relation to colony-housing opportunities created by nuts and nest-site choice. Our results indicated that species diversity and nut occupancy rates do not differ among sites or states and that ant-occupied nuts are spatially aggregated across ant species, a pattern inconsistent with spatial segregation of species that might arise in a competition-assembled community. We tested the ability of artificial nest cavities ("Mobile Artificial Ant Pods", MAAPs) to attract ant colonies, a method for sampling the ant fauna in litter. MAAP occupancy rates were similar to occupancy rates for nearby nuts.

1.2 INTRODUCTION

Many species of ants (Hymenoptera: Formicidae) nest in the fallen nuts of trees. Fallen nuts provide ready-made and protected ant nesting sites. Nuts suitable for ant colonization must have an entrance, such as a crack or holes made by seed predators. We estimate nuts of over 30 species of southeastern trees including hickories, pecans, chestnuts, walnuts, and oaks provide nesting sites for ants. Nut-nesting ants provide research opportunities such as discrete spatial units for sampling (MacGown 2006), colony structure (Duffield and Alpert 2011, Foizik and Heinze 1998, Talbot 1957), demography (Backus and Herbers 2009), correlations to site-specific environmental preferences (Greenslade 1971), competition (Scharf et al. 2011), nut choice (Pratt

and Pierce 2001), and effects of volume constraints on colony structure (Foitzik and Heinze 1998, Cao and Dornhaus 2008, Herbers and Banschbach 1995). However, there is still a dearth in knowledge of biogeographic distribution and diversity in nut-nesting ant communities.

1.3 METHODS

Nut Collections: (**Figure 1.1**) We collected 6741 nuts on the forest floor under 68 trees representing nine species in two families: black walnut (*Juglans nigra* L., n=8), hickories (*Carya glabra* (Mill.) Sweet*, Carya illinoinensis* (Wangenh.) K. Koch, *C. ovata* (Mill.) K. Koch, *C. myristiciformis* (F. Michx.) Nutt. and *C. tomentosa* (Poir.) Nutt., n=52), (Juglandaceae), and oaks (*Quercus alba* L.*, Q. nigra* L.*,* and *Q. rubra* L., n=8) (Fagaceae) across five states (GA, MD, MS, NC, TN). We defined a site as the area of ground underneath the canopy of a single tree. We collected nuts in forests of states near authors' residences where authors had previously obtained collecting permits or where collecting permits were not required. We chose individual sites upon discovery of a nut-bearing tree species and presences of nuts on the forest floor, and we gave no preference of species or size of tree. For only two trees did we collect all nuts found (**Table 1.1**). For all other trees, we collected a subset of nuts that could be occupied, *i.e*., those with entrances suitable for ants. We collected 13 to 375 nuts in individual bags per tree (site). For two sites, we collected all nuts that we found, with or without entrances to determine the number of unavailable nuts that could be occupied (**Table 1.1**).

We collected nuts and placed and retrieved artificial nests we termed Mobile Artificial Ant Pods (MAAPs) in the following places (listed in **Table 1.1** with geographic coordinates): BLND-Blandy Experimental Farm, Clarke Co. VA; CIV-Rockville Civic Center, Montgomery Co. MD; CJMD-Cabin John Regional Park, Montgomery Co. MD; FDR-FDR State Park, Meriweather

Co. GA; ELJY-Elijay, Gilmer Co. GA; GlFR-Glen Forest Rd, Knox Co. TN; KEO-Keown Falls, Walker Co. GA; LFSK-Highlands, NC; NOX-Noxubee Wildlife Preserve, Winston Co. MS; OCNF-Oconee National Forest, Greene Co. GA; PIN-Chestnut Mt. Shooting Range, Gordon Co. GA; PMFH-Pigeon Mt., Walker Co. GA; RKLV-Rockville, Cabin John Regional Park, Montgomery Co. MD; SAP-Sapelo Island, McIntosh Co. GA; SCNC-Sandy Creek Nature Center, Clarke Co. GA; SES-Sessums, Oktibbeha Co. MS; Tom-Tombigbee State Park, Winston Co. MS; and WXY-Waldoxy State Park, Marshall Co. MS (**Figure 1.1**)

Spatial Dispersion of Ants at Walnut Tree: We mapped, collected, and labeled all nuts that were suitable for ant nests within a circular area defined by a 10 m radius from the base of a black walnut tree in Athens, Clarke County, Georgia. We then recorded nut locations and ant entrance types (e.g. exit holes created by other insects, feeding damage caused by mammal feeding).

Artificial nest design and Placement (**Figure 1.2**): Booher and Duffield designed artificial ant nests (MAAPs) based on a similar earlier design by Duffield and Alpert (2011). Michael Oliveri Studios, Athens, GA (michaeloliveri.com) produced MAAPs using a computer controlled router (CNC) to cut reclaimed hickory and oak to make the MAAPs. MAAPs measured 6.1 cm in length, 3.5 cm in width, and 1.2 cm in height. Each MAAP contained two, stepped column shaped cavities. Each stepped cavity contained a nesting cavity (8 mm deep x 13 mm diameter) and a slightly larger cavity directly above the nesting cavity to hold a cover slip (using Elmer's wood glue) and a ¾ inch oak button plug (purchased from widgetco.com). We drilled entrance holes either 1.5 or 3 mm in diameter into either the short or the long side of the MAAPS.

Placement of the MAAP artificial traps (**Figure 1.2**): To place traps, we looped monofilament line through a drilled hole in one MAAP corner and placed steel wire stake flags through the monofilament loop. We put out 17 sets of MAAPs during the spring and summer of 2013.

Sixteen sets had 50 MAAPs spaced 1 m apart in a 5 x 10 m array. For six of these 16 arrays, we collected nuts within 25 meters of six MAAP arrays to compare pairwise frequency use of MAAPs (paired sites listed in **Table 1.1** for test in **Figure 1.8**). We collected all arrays of MAAPs between 6 and 10 weeks after placement. We did not initially suspect ant colonization preference of either hickory or oak made MAAPs and therefore did not preferentially place either type of MAAP at or within any site. Upon recovery of MAAPs, we recorded what type of wood each MAAP was made of for fourteen of the sixteen 5 x 10 m arrays as well as recorded the size and placement of drilled entrance hole. We failed to record these data on eight of 700 recovered MAAPs from the fourteen investigated sites. These eight MAAPs had excessive termite damage, extreme fungal growth or decay, or were broken presumably due to deer stepping on them. These MAAPs contained no ants and were not used in contingency analyses (**Table 1.2** and **Table 1.3**).

For the 17th set of MAAPs, we replaced all of the walnuts collected around the base of a black walnut tree with MAAPs. We collected this set of 328 MAAPs in September 2015 and is the seventh site we used for paired comparison of MAAP and nut occupancy frequency.

Statistical Methods: To determine if distributions of data were normal, we visually inspected histograms and theoretical quantile plots (QQ plots) (Team RC 2015). Because no data fit Gaussian distribution assumptions, we used medians and mean absolute value around the medians to describe central tendencies. Small non-normal data sets required that we use nonparametric tests based on ranks. We used bootstrapping statistical techniques on ranked and non-ranked data to produced confidence intervals, measured effect sizes, and provided associated p-values. We compared the rank abundance of species across states using JMP® software to

perform a Wilcoxon test (JMP® 1989-2016). We wrote custom *R* scripts for bootstrapping analyses (Team RC 2015). To generate confidence intervals on nearest neighbor analyses to determine whether ants are under or over-dispersed, Hubbell performed an analysis using custom Basic script. We generated rarefaction curves using *R* package BiodiversityR (Kindt 2005). We chose Fisher's alpha to compare site diversity, as it is a relatively sample-size independent measure of diversity. Because sample sizes were small and not Gaussian in distribution, we used mean ranks to evaluate the similarities of occupancy for pairs of MAAP and nut collection sites. We performed Pearson Chi Square (X^2) contingency analyses in JMP® for observations cross-classified by two sets of nominal categories to test whether categorical data was greater or less than expected for ant colonization of MAAPs and report Pearson X^2 statistics (JMP® 1989-2016).

Identification: MacGown and Booher identified species and deposited vouchers in the Mississippi Entomological Museum (MEM) and the University of Georgia Collection of Arthropods (UGCA).

1.4 RESULTS

1.4.1 Frequencies, Abundances, and Diversities of Nut-nesting Ant Communities

Thirty-six ant species occupied 10.1±4.2% n=68 (site median, median absolute deviation, sample size) of nuts over all tree sites (**Figure 1.3**). Percentage of occupied nuts did not vary significantly between states or regional sites (GA=9.6±4.4% n=12, MD=10.2±4.0% *n*=37, MS=10.0±4.9% n=17, TN=7.7% n=1, NC=11.2% *n*=1; Wilcoxon, one way ranked test between GA, MD, MS, NC, and TN, $X^2 = 0.62$, $p = 0.97$, and between sites, $X^2 = 9.63$, $p = 0.79$. Fifteen ant species colonized 9.2% (104) of the 1128 MAAPs recovered. Though some MAAPs had decayed more than others and some had been damaged, it is of interest to note is that all MAAPs

were recovered at time of removal due to the ease of finding staked flags that held MAAPs in place.

The range of occupancy was 0-42% of nuts by ants at a given tree site. Ant species richness was similar at state level (GA=20, MD=18, MS=16), but despite similar species richness, paired states share only 14% (MS and MD) to 31% (GA and MS) of ant species, and all three states shared only four of the 36 nut-nesting ant species. Fisher's alpha (diversity) did not differ between state, site, or tree species (Wilcoxon, one way ranked test, states $X^2 = 2.59$ $p = 0.46$, sites $X^2 = 9.82$ $p = 0.56$, and tree species $X^2 = 12.34$ $p = 0.14$). Of note, we collected the social parasite *Vollenhovia nipponica* Kinomura and Yamauchi in a colony of brachypterous *V. emeryi* Wheeler queens, and long winged *V. emeryi* in a colony with brachypterous *V. emeryi* queens nesting in walnuts in Rockville, MD. These ants are native to Japan, and these are the first collections of *V. nipponica* and long winged *V. emery* in the United States (**Figure 1.4**, G, H) (Kinomura et al. 1992, Kubota 1984, Wetterer et al. 2015).

The species accumulation curve (red) generated by actual sampling method predicts a higher initial accumulation (but not significant) than if all nuts from all states were randomly sampled in sets of 100 nuts (black) (**Figure 1.5**).

1.4.2 Density and dispersion of ants at a walnut tree

This study site contained the highest number of species (n=10) and included two invasive species, the Red Imported Fire ant (*Solenopsis invicta* Buren) and the Asian Needle Ant (*Brachyponera chinensis* Emery). Nearest neighbor comparisons between occupied and unoccupied walnuts showed that ant colonies were aggregated (**Figure 1.6, Figure 1.7**).

1.4.3 MAAPs versus nuts for occupancy by ants.

Species colonized 8.0±6.0% MAAPs of the seven paired sites, and three species that were not collected in nuts colonized MAAPS: *Odontomachus brunneus* (Patton)*, Strumigenys creightoni* Smith*, and Strumigenys louisianae* Roger. In secondary sampling of MAAPs that replaced all walnuts, ants occupied (10.1%) of MAAPs, which was the same as colonized nuts. Again, we observed the same species richness (10 species) and diversity (fisher's alpha = 4.88), yet only 60% of species present in walnuts were present in MAAPs (Jaccard's Index = 0.43).

MAAPs attracted more ants under trees where more ants used nuts. The paired sites with highest and lowest median occupancy frequency fall outside the upper and lower 95% confidence intervals (Mean Rank Transformed mean frequencies per paired site **Figure 1.8**, one-way ANOVA $F = 7.48$, $p = 0.009$). Species collected in both MAAPs (with number of times collected) that were also collected in nuts are *Aphaenogaster carolinensis* Wheeler (*n*=20), *Temnothorax curvispinosus* (Mary) (n=10), *Nylanderia faisonensis* (Forel) (*n*=14), *Strumigenys rostrata* Emery (*n*=11), *Myrmica punctiventris* Roger (*n*=6), *Strumigenys ohioensis* Kennedy and Schramm (*n*=3), *Lasius alienus* (Foerster) (*n*=1), and *Solenopsis carolinensis* Forel (*n*=1). Species only collected in MAAPS are *Strumigenys creightoni* (*n*=1) and *Strumigenys louisianae* (*n*=1). Of the investigated 692 MAAPs, we found MAAPs made of hickory had higher occupancy than those made of oak ($X^2 = 29.81$, $p < 0.001$, $n = 692$, **Figure 1.2**), and ants were more likely to colonize MAAPs with diameter entrance holes (3mm verses 1.5mm, $X^2 = 14.12$, $p < 0.001$, $n = 692$, **Table 1.3**).

1.5 DISCUSSION

Many ants we observed inhabiting nuts might only rarely use nut cavities or do so for brief periods. Soil nesting species such as *Solenopsis invicta* are common where they occur in our

sampled sites, but they rarely occupied nuts. However, nuts may be a vital resource for the most common or site abundant ants that utilize cavities for nesting resources. We found that numerous queens of larger species that occupied nuts had few workers, suggesting these queens are likely using nuts for founding colonies, but quickly relocating as their colonies outgrew the limited space (*e.g. Camponotus chromaoides* Bolton*, C. subbarbatus* Emery*,* and *Crematogaster lineolata* (Say)). The most common species in this study, *Nylanderia faisonensis,* likely uses available nuts to house only portions of its colony at any given time. In most nuts containing this species that we observed, larvae and workers were found under the nut and in the surrounding leaf litter. In contrast, a few species were cavity-dwelling specialists with colonies completely contained within nuts (*e.g. T. curvispinosus* and *Strumigenys rostrata* (**Figure 1.4**: E, F). Several rare or uncommonly collected species were abundant at some sites including *Nylanderia trageri* Kallah and LaPolla*, Vollenhovia emeryi, Temnothorax tuscaloosae* (Wilson) (**Figure 1.4**: A, G, C), as well as other infrequently collected species that occur in low abundance and are likely to make nests in sites other than available nuts.

The availability of nuts suitable for ants to nest in are limited by variation in the number of nuts produced by a tree and the decomposition of nuts, or ecological factors (such as density dependence and environmental preference) may limit the nuts that ant species colonize. Species such as *V. emeryi* and *T. tuscaloosae* had high abundances in riparian forests, but rarely occupied nuts outside of this narrow ecological range. Though there is much variation in percent nut occupancy under different trees, there is a median central tendency of only 10% colonization of nuts with ready-made entrances. Because none of these species found in this study are known to bore entrance holes in nuts, they are limited to nuts already having entrances. Most nut-bearing tree species of the southeastern U.S. have inter-annual cycles of seed production, with high-

production “mast” years, separated by one or more years of low production. This variation in seed production may be adaptive as a predator-satiation phenomenon, favored by selection because more seeds are produced and survive in mast years than can be consumed by seed-predating insects (Vander Wall 2001). Seed-predating insects provide entrance holes and empty nut cavities when they emerge and provide many of the highest quality ready-made nuts for ant colonization. Variation in colonization may be due to seed-predating insect population levels, variation in the number of nuts produced by trees, and the stability of available nuts for ant colonization. At the two trees that we counted all nuts having entrances or being absent of entrances, less than half of nuts had entrances and were unavailable for ants to colonize. More dynamic data on nut production, seed-boring predators, nut availability, and changes in diversity and abundance of ants is needed to give biological meaning to our observed frequency of ant occupancy in nuts.

Ants that nest in nuts could serve as model systems to test hypotheses of community organization in structured habitats. Colonies in nuts are easy to find, map, and manipulate, and nuts are spatially distributed critical resources. The aggregation of ants (**Figure 1.7**) predict environmental factors, rather than competition, organize the dispersion of ants. Nevertheless, competition may still play some role in ant dispersal and colony founding within resource-rich areas within sites. Using MAAPs and nuts to manipulate densities through the addition and removal of both colonies and nesting opportunities promises to enhance understanding of community organization in nut-nesting ants.

1.6 List of Figures

Figure 1.6. A map of fallen walnuts with entrances under the canopy of a walnut tree in Georgia. The large centered black circle represents the trunk of the tree.

Figure 1.7. Nearest neighbor analysis of all nuts with entrances from the base of a black walnut tree in Georgia. The two lines shown represent separate regressions of average nearest neighbors from n1 to n30 for an occupied nut to its nearest neighboring occupied nut (blue, bottom line), and a nut chosen at random to its nearest neighbor (from n1 to n30, perm=100 times). The bars above and below are 95% confidence limits on the means, showing the significance of non-overlap between paired nuts.

Figure 1.8. Rank transformed mean nut and MAAP nesting frequencies of ants at the same site. Ant colonization frequency is similar in MAAPs and nuts at the same site. Site abbreviations refer to geographic locations and correspond to sites where we also collected nuts (**Table 1.1**). Site abbreviations are as follows: SCNC-Sandy Creek Nature Center, Clarke Co. GA; Tom-Tombigbee State Park, Winston Co. MS; WXY-Waldoxy State Park, Marshall Co. MS; and NOX-Noxubee Wildlife Preserve, Winston Co. MS; OCNF-Oconee National Forest, Greene Co. GA.

1.7 List of Tables

Table 1.1. Lists sites where MAAPs and nuts were collected.

Sites: BLND-Blandy Experimental Farm, Clarke Co. VA.; CIV-Rockville Civic Center, Montgomery Co. MD; CJMD-Cabin John Regional Park, Montgomery Co. MD; FDR-FDR State Park, Meriweather Co. GA; ELJY-Elijay, Gilmer Co. GA; GlFR-Glen Forest Rd, Knox Co.

TN; KEO-Keown Falls, Walker Co. GA; LFSK-Highlands, NC; NOX-Noxubee Wildlife Preserve, Winston Co. MS; OCNF-Oconee National Forest, Greene Co. GA; PIN-Chestnut Mt. Shooting Range, Gordon Co. GA; PMFH-Pigeon Mt., Walker Co. GA; RKLV-Rockville, Cabin John Regional Park, Montgomery Co. MD; SAP-Sapelo Island, McIntosh Co. GA; SCNC-Sandy Creek Nature Center, Clarke Co. GA; SES-Sessums, Oktibbeha Co. MS; TOM-Tombigbee State Park, Winston Co. MS; WXY-Waldoxy State Park, Marshall Co. MS. Collector abbreviations are D = R.M. Duffield, B = D.B. Booher, and M = J.A. MacGown

Table 2. Pearson Chi Square Table of Occupied MAAPs by wood species.

Table 3. Pearson Chi Square Table of Occupied MAAPs by entrance diameter.

1.8 Figures and Tables

Figure 1.

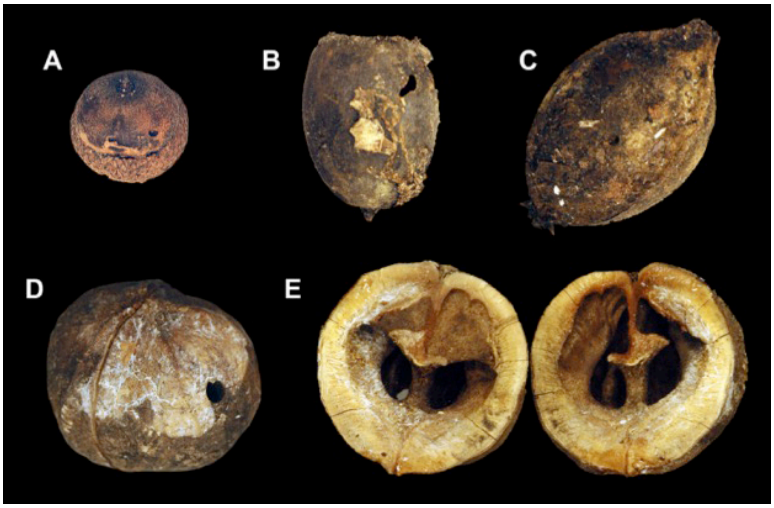


Figure 2.

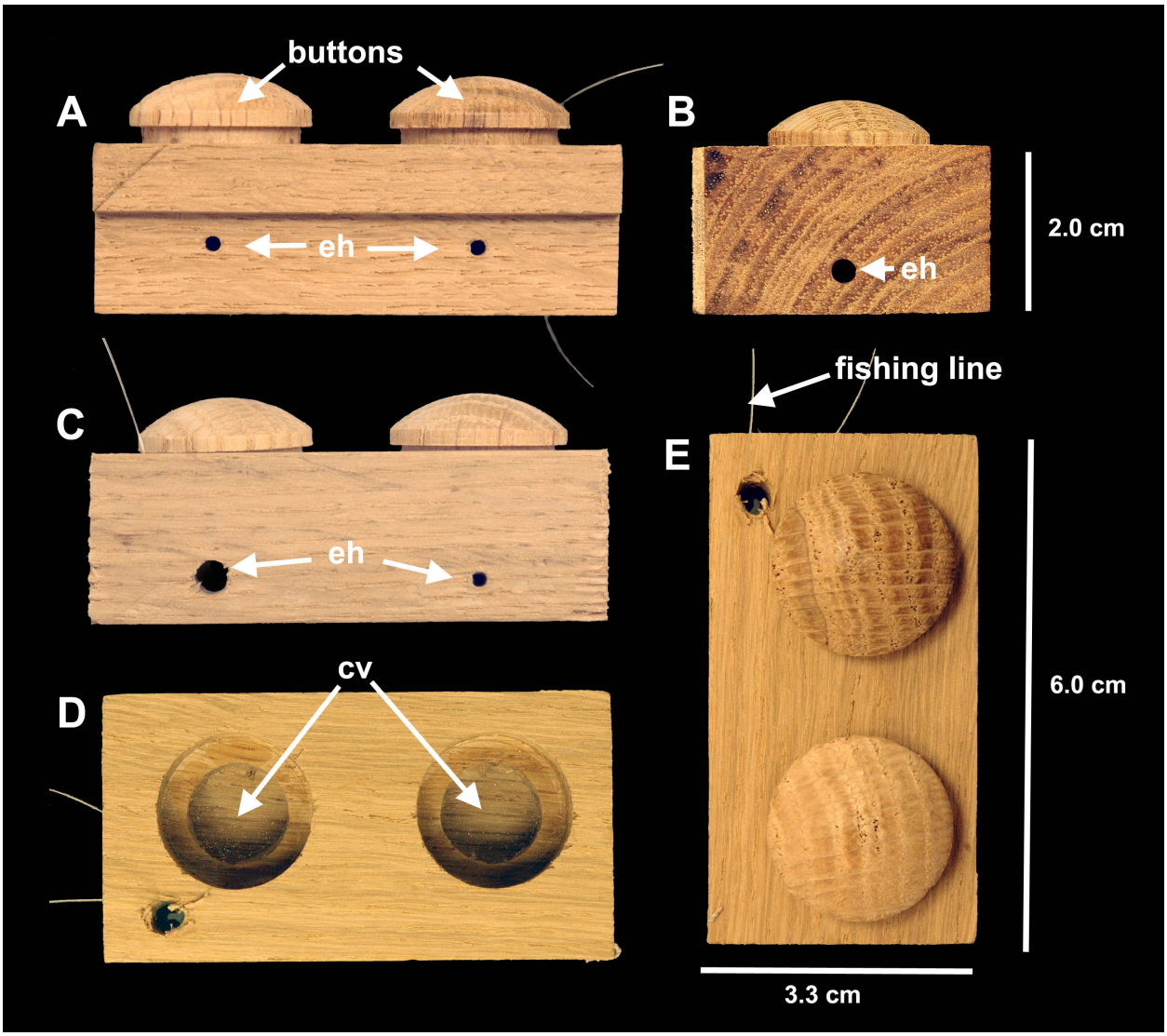


Figure 3.

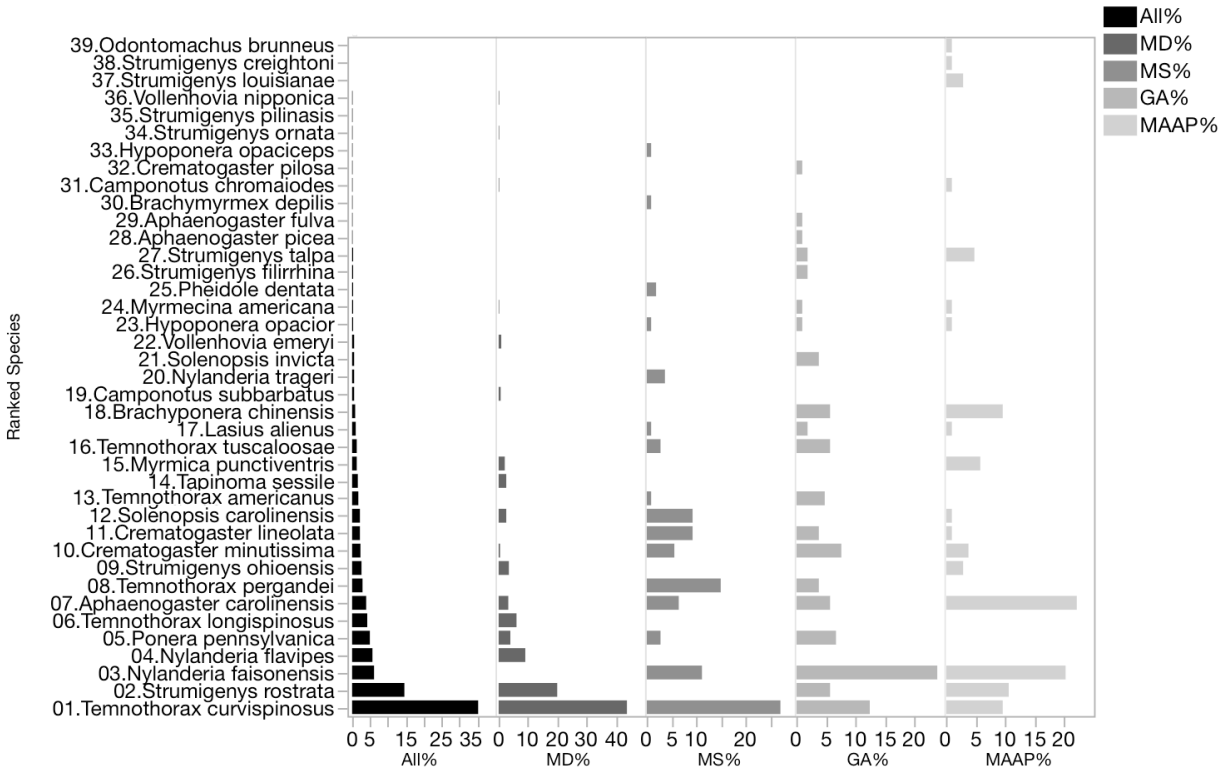

All%
MD%
MS%
GA%
MAAP%
Ranked Species
39.Odontomachus brunneus
38.Strumigenys creightoni
37.Strumigenys louisianae
36.Vollenhovia nipponica
35.Strumigenys pilinasis
34.Strumigenys ornata
33.Hypoponera opaciceps
32.Crematogaster pilosa
31.Camponotus chromaiodes
30.Brachymyrmex depilis
29.Aphaenogaster fulva
28.Aphaenogaster picea
27.Strumigenys talpa
26.Strumigenys filirrhina
25.Pheidole dentata
24.Myrmecina americana
23.Hypoponera opacior
22.Vollenhovia emeryi
21.Solenopsis invicta
20.Nylanderia trageri
19.Camponotus subbarbatus
18.Brachyponera chinensis
17.Lasius alienus
16.Temnothorax tuscaloosae
15.Myrmica punctiventris
14.Tapinoma sessile
13.Temnothorax americanus
12.Solenopsis carolinensis
11.Crematogaster lineolata
10.Crematogaster minutissima
09.Strumigenys ohioensis
08.Temnothorax pergandei
07.Aphaenogaster carolinensis
06.Temnothorax longispinosus
05.Ponera pennsylvanica
04.Nylanderia flavipes
03.Nylanderia faisonensis
02.Strumigenys rostrata
01.Temnothorax curvispinosus
0 5 15 25 35
All%
0 10 20 30 40
MD%
0 5 10 20
MS%
0 5 10 15 20
GA%
0 5 10 15 20
MAAP%

Figure 4.

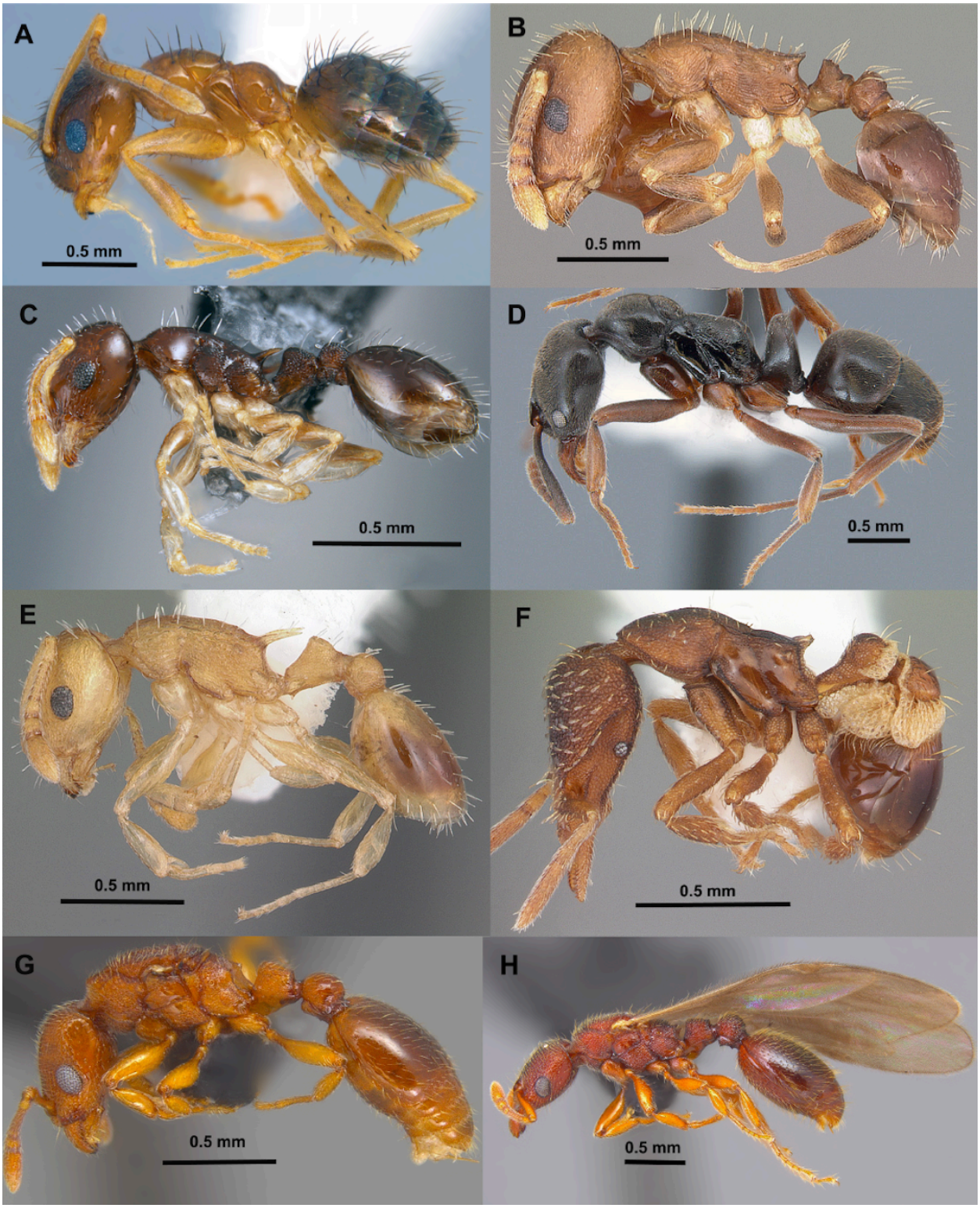
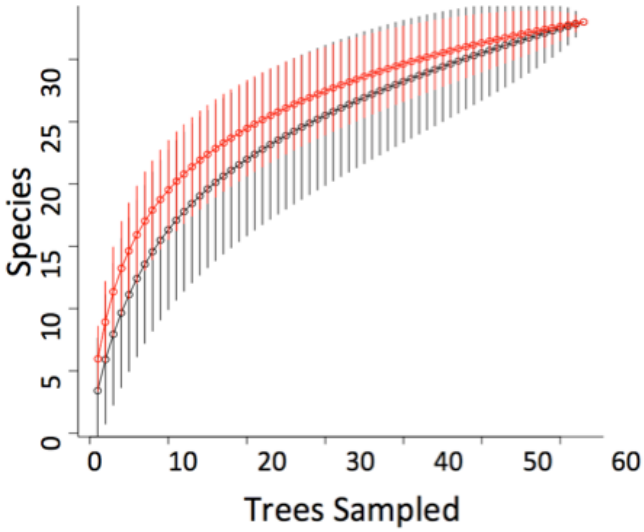


Figure 5.



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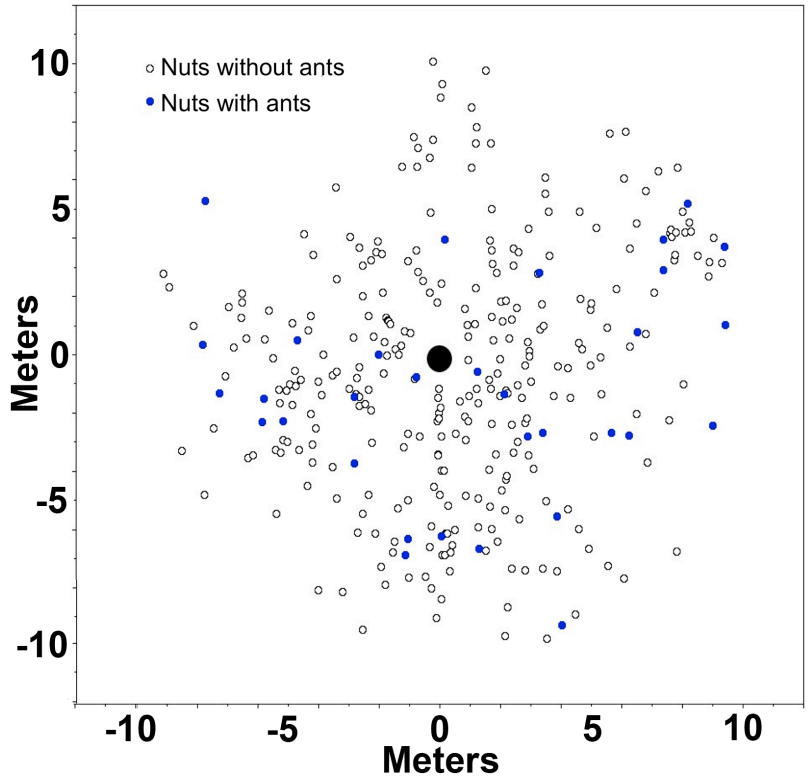

Figure 7.

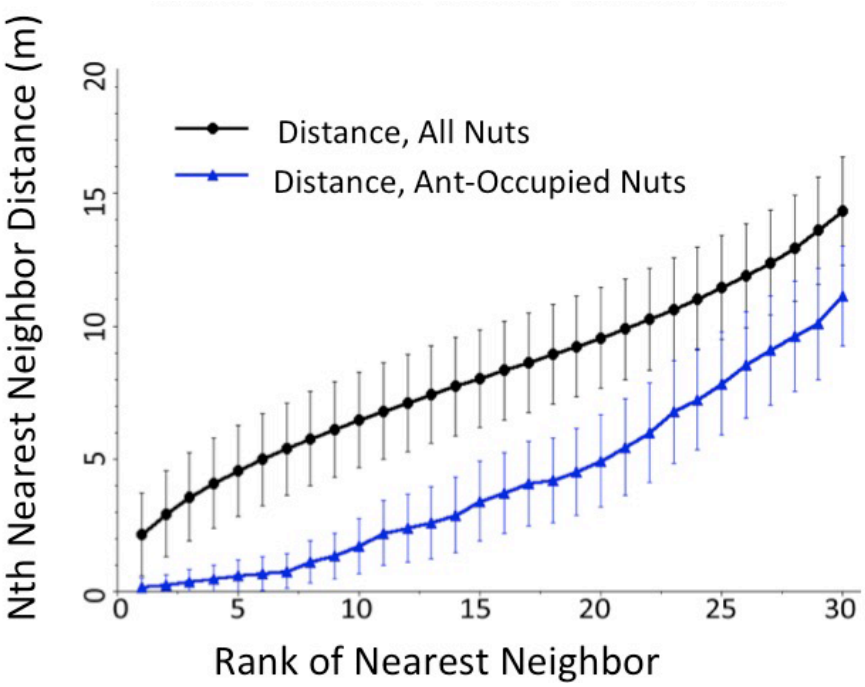

Figure 8.

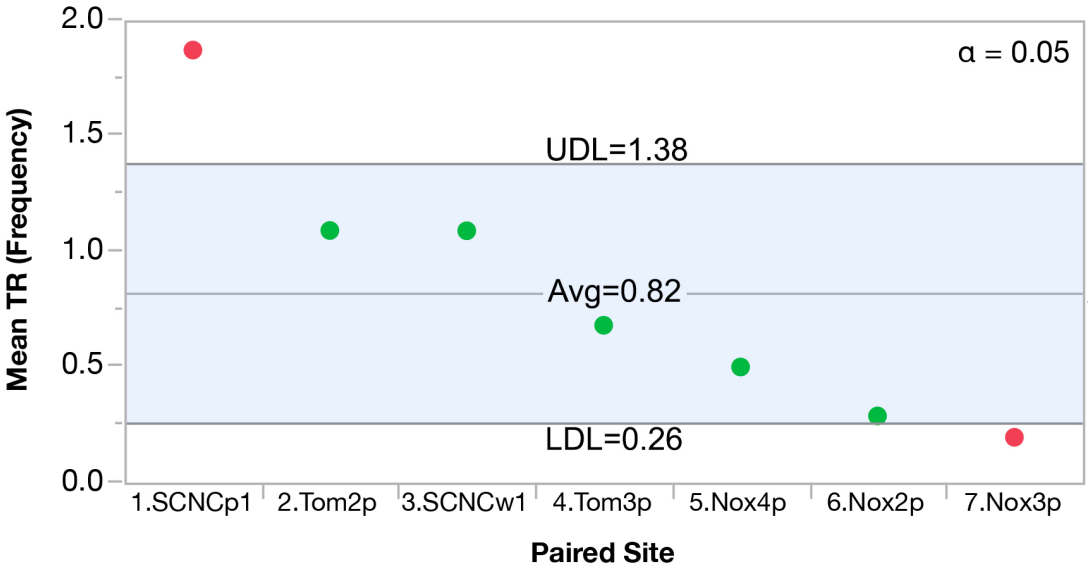

Table 1. Collections and Occupancies of Nuts and MAAPs

State	Nut Site	Lat N	Lon W	nut species/MAAP	coll.	Paired MAAP array	Total Nuts	Nuts W/Ent	Occ. Nuts	Percent Occ.
GA	ELJY-W1	34.722	84.505	Juglans nigra	B & D		NA	12	4	33.30%
GA	PMPL-W1	34.669	85.390	Juglans nigra	B & D		NA	62	18	29.00%
GA	PMFH-W1	34.669	85.390	Juglans nigra	B & D		NA	38	7	18.40%
GA	SCNC-01	33.989	83.380	Quercus nigra	B	SCNCp1	NA	50	6	12.00%
GA	SCNC-W1	33.982	83.381	Juglans nigra	B	SCNCw1	NA	328	33	10.10%
GA	PMFH-H1	34.669	85.390	Carya sp.	B & D		NA	72	6	8.30%
GA	OCNF-H1	33.734	83.270	Carya glabra	B		NA	25	2	8.00%
GA	SCNC-O5	33.983	83.383	Quercus rubra	B		NA	25	0	0.00%
GA	SCNC-O6	33.986	83.384	Quercus rubra	B		NA	25	0	0.00%
GA	DBBC_5073	32.862	84.702	Carya tomentosa	B		95	36	3	8.30%
GA	PIN_05	34.613	85.047	Carya sp.	B		NA	33	3	9.10%
GA	KEO_03	34.613	85.087	Carya sp.	B		NA	145	23	15.90%
MD	CJMD-H24	39.035	77.152	Carya sp.	D		NA	85	36	42.40%
MD	CJMD-H15	39.035	77.152	Carya sp.	D		NA	50	17	34.00%
MD	CJMD-H27	39.035	77.152	Carya sp.	D		NA	40	9	22.50%
MD	CJMD-H5c	39.035	77.152	Carya sp.	D		NA	68	15	22.10%
MD	CJMD-H21	39.035	77.152	Carya sp.	D		NA	19	4	21.10%
MD	CJMD-H22	39.035	77.152	Carya sp.	D		NA	80	16	20.00%
MD	CJMD-H18	39.035	77.152	Carya sp.	D		NA	205	36	17.60%
MD	CJMD-H19	39.035	77.152	Carya sp.	D		NA	85	13	15.30%
MD	BLND-W3	39.051	78.063	Juglans nigra	B & D		NA	40	6	15.00%
MD	CJMD-H23	39.035	77.152	Carya sp.	D		NA	40	6	15.00%
MD	CJMD-H25	39.035	77.152	Carya sp.	D		NA	120	17	14.20%
MD	BLND-W1	39.051	78.063	Juglans nigra	B & D		NA	80	11	13.80%
MD	CJMD-H20	39.035	77.152	Carya sp.	D		NA	140	18	12.90%
MD	CJMD-H17	39.035	77.152	Carya sp.	D		NA	75	9	12.00%
MD	CJMD-H14	39.035	77.152	Carya sp.	D		NA	230	25	10.90%
MD	CJMD-H9	39.035	77.152	Carya sp.	D		NA	75	8	10.70%
MD	CJMD-H10	39.035	77.152	Carya sp.	D		NA	85	9	10.60%
MD	CJMD-H1	39.035	77.152	Carya sp.	D		NA	59	6	10.20%
MD	CJMD-H36	39.035	77.152	Carya sp.	D		NA	120	12	10.00%
MD	CJMD-H3	39.035	77.152	Carya sp.	D		NA	143	14	9.80%
MD	CJMD-H4	39.035	77.152	Carya sp.	D		NA	187	17	9.10%
MD	CJMD-H5a	39.035	77.152	Carya sp.	D		NA	178	15	8.40%
MD	CJMD-H7	39.035	77.152	Carya sp.	D		NA	208	16	7.70%
MD	CJMD-H8	39.035	77.152	Carya sp.	D		NA	110	8	7.30%

MD	CJMD-H13	39.035	77.152	Carya sp.	D		NA	100	7	7.00%
MD	CJMD-H6	39.035	77.152	Carya sp.	D		NA	230	16	7.00%
MD	CJMD-H2	39.035	77.152	Carya sp.	D		NA	30	2	6.70%
MD	BLND-W2	39.051	78.063	Juglans nigra	B & D		NA	62	4	6.50%
MD	CJMD-H11	39.035	77.152	Carya sp.	D		NA	135	8	5.90%
MD	CJMD-H35	39.035	77.152	Carya sp.	D		NA	300	17	5.70%
MD	CJMD-H33	39.035	77.152	Carya sp.	D		NA	95	5	5.30%
MD	CJMD-H5b	39.035	77.152	Carya sp.	D		NA	123	5	4.10%
MD	CJMD-H26	39.035	77.152	Carya sp.	D		NA	100	4	4.00%
MD	CJMD-H16	39.035	77.152	Carya sp.	D		NA	245	6	2.40%
MD	CJMD-H34	39.035	77.152	Carya sp.	D		NA	375	7	1.90%
MD	CJMD-H12	39.035	77.152	Carya sp.	D		NA	90	1	1.10%
MD	CIV-08	39.088	77.127	Juglans nigra	D & B		NA	40	5	12.50%
MS	NOX-H4	33.230	88.910	Carya glabra	B & M		NA	38	12	31.60%
MS	TOM-H7	33.218	89.096	Carya ovata	D		NA	100	17	17.00%
MS	NOX-O4	33.230	88.910	Quercus alba	B & M		NA	86	14	16.30%
MS	SES-H1	33.394	88.711	Carya myristiciformis	M		NA	32	5	15.60%
MS	TOM-02	33.218	89.096	Carya ovata	M		NA	13	2	15.40%
MS	NOX-H7	33.230	88.910	Carya ovata	D		NA	28	4	14.30%
MS	WXY-H2	34.660	89.465	Carya glabra	D		NA	62	7	11.30%
MS	TOM-H1	33.218	89.096	Carya glabra	M		NA	105	11	10.50%
MS	TOM-H3	33.218	89.096	Carya sp.	D & B	Tom3p	NA	50	5	10.00%
MS	TOM-O2	33.218	89.096	Quercus nigra	M	Tom2p	NA	67	7	10.45%
MS	WXY-H1	34.660	89.465	Carya glabra	D & B		NA	86	8	9.30%
MS	NOX-O4	33.230	88.910	Quercus alba	M	Nox4p	NA	100	7	7.00%
MS	TOM-O1	33.218	89.096	Quercus alba	M		NA	101	6	5.90%
MS	TOM-O4	33.218	89.096	Quercus alba	B & M		NA	51	1	2.00%
MS	NOX-H3	33.230	88.910	Carya sp.	D	Nox3p	NA	61	1	1.60%
MS	NOX-H2	33.230	88.910	Carya sp.	D	Nox2p	NA	20	0	0.00%
MS	TOM-O1	33.218	89.096	Carya sp.	D & M		NA	50	0	0.00%
NC	LFSK-H1	35.045	83.186	Carya illinoinensis	B		NA	39	3	7.70%
TN	GlFR-01	35.946	83.970	Carya sp.	B		790	367	41	11.20%
GA	SCNC p1	33.989	83.380	MAAP array	D & B	-	-	50	9	18.00%
GA	SCNC p2	33.989	83.380	MAAP array	D & B	-	-	50	10	20.00%
GA	SCNC p3	33.989	83.380	MAAP array	D & B	-	-	50	8	16.00%
GA	SCNC p4	33.989	83.380	MAAP array	D & B	-	-	50	14	28.00%
MS	Tom 1p	33.218	89.096	MAAP array	D, B, & M	-	-	50	0	0.00%
MS	Tom 2p	33.218	89.096	MAAP array	D, B, & M	-	-	50	5	10.00%

MS	Tom 3p	33.218	89.096	MAAP array	D, B, & M	-	-	50	3	6.00%
MS	Tom 4p	33.218	89.096	MAAP array	D, B, & M	-	-	50	1	2.00%
MS	Nox1p	33.230	88.910	MAAP array	D, B, & M	-	-	50	7	14.00%
MS	Nox2p	33.230	88.910	MAAP array	D, B, & M	-	-	50	2	4.00%
MS	Nox 3p	33.230	88.910	MAAP array	D, B, & M	-	-	50	0	0.00%
MS	Nox 4p	33.230	88.910	MAAP array	D, B, & M	-	-	50	1	2.00%
MS	Nox 5p	33.230	88.910	MAAP array	D, B, & M	-	-	50	2	4.00%
MD	RKLV-01	39.035	77.152	MAAP array	D	-	-	50	5	10.00%
MD	RKLV-02	39.035	77.152	MAAP array	D	-	-	50	0	0.00%
GA	SAP p1	31.403	81.284	MAAP array	D & B	-	-	50	4	8.00%
GA	SCNC W1	33.982	83.381	MAAP array	D & B	-	-	328	33	10.06%

Table 2.

Site	N Hickory	N Oak	N Hickory Occupied	N Oak Occupied	Sample Size	X^2	Prob > X^2
Nox1	21	28	3	4	49	0	1
Nox2	32	17	2	0	49	1.11	0.29
Nox3p	33	17	0	0	50	-	-
Nox4p	2	48	1	1	50	11.48	<0.001
Nox5	10	40	1	1	50	1.17	0.28
Nox6	0	49	-	0	49	-	-
SCNCp1	30	20	9	1	50	4.69	0.03
SCNCp2	11	38	4	5	49	3.06	0.08
SCNCp3	29	19	8	0	48	6.29	0.01
SCNCp4	17	33	6	8	50	0.69	0.41
Tom1p	28	20	0	0	48	-	-
Tom 2	7	43	6	0	50	41.88	<0.001
Tom3	19	31	3	0	50	5.21	0.02
Tom4	10	40	1	0	50	0.26	0.61
Total	249	443	44	20	692	29.81	<0.001

Table 3.

Site	N 3 mm ent.	N. 1.5 mm ent.	N 3 mm occupied	N 1.5 mm Occupied	Sample Size	X^2	Prob > X^2
Nox1	32	17	4	3	49	0.24	0.62
Nox2	39	10	2	0	49	0.54	0.47
Nox3p	29	21	0	0	50	-	-
Nox4p	41	9	2	0	50	0.46	0.5
Nox5	32	18	1	1	50	0.18	0.67
Nox6	25	24	0	0	49	-	-
SCNCp1	30	20	9	1	50	4.69	0.03
SCNCp2	29	20	7	2	49	1.58	0.21
SCNCp3	29	19	8	0	48	6.29	0.01
SCNCp4	29	21	10	4	50	1.44	0.23
Tom1p	27	21	0	0	48	-	-
Tom 2	20	30	6	0	50	10.852	0.001
Tom3	31	19	3	0	50	1.96	0.16
Tom4	31	19	1	0	50		
Total	424	268	53	11	692	14.12	<0.001

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2. Chapter 2. Pilot investigations on the feasibility of studying *Strumigenys* ant communities

2.1 ABSTRACT

Species of the ant genus *Strumigenys* overlap nearly completely in diet and several species often occur in the same square meter of leaf litter habitat. Because *Strumigenys* are abundant and diverse in the southeastern United States, they are potentially a good taxon in which to test hypotheses about the maintenance and organization of community assemblages. However, there are no published studies of *Strumigenys* communities, so before one can ask community assembly questions, one must first describe *Strumigenys* assemblages. My first descriptive goal was to develop collection and sampling methods to assess the feasibility of studying *Strumigenys* communities. My second goal was to describe the abundance and diversity of *Strumigenys* in typical southeastern United States habitats. My third goal was to frame hypotheses of alternative mechanisms to explain *Strumigenys* community assembly.

I randomly sampled 0.20 ha sites for *Strumigenys* living in leaf litter in a topographically heterogeneous 80 ha nature preserve in Athens, GA. To accomplish this I 1) tested the efficiency of two litter-extraction methods; 2) subsampled leaf litter to extract *Strumigenys*; 3) took a set of environmental measurements and observations in each 0.20 ha site likely to be important to *Strumigenys*; 4) tested the null hypothesis that *Strumigenys* ant species have no environmental preferences and will inhabit all sites and habitats randomly; and 5) randomly sampled 20 one-m^2 sites in the most diverse 0.20 ha sites, assuming the same null hypothesis.

There were no statistically significant differences in diversity or abundance of *Strumigenys* between Winkler and Berlese extraction methods. I rejected the null hypotheses that *Strumigenys* have no environmental preference and occur in all environments and sites with equal probability. Both in 0.20 ha sites and in 1.0 m^2 microsites, *Strumigenys* co-occurred more often than expected

under the null hypothesis, suggesting that *Strumigenys* species have similar habitat preferences. Both 0.20 ha habitats and 1.0 m^2 microsites are appropriate spatial scales for investigating abiotic factors and general habitat characteristics important for *Strumigenys* communities. However, I concluded that an even finer scale (< 1.0 m^2) would be necessary to investigate community patterns on spatial scales on which *Strumigenys* are likely to interact or compete.

2.2 INTRODUCTION

2.2.1 The ant genus *Strumigenys*

Strumigenys are the most diverse genus of ants occurring in southeastern forests of the United States. Yet, until methods of litter-extraction became popular in the 1960's, these ants were rarely collected. Even with improved collecting techniques that are now commonly used to sample litter dwelling ants, *Strumigenys* are still often underreported (Deyrup and Cover 2009). This underrepresentation is likely due to a combination of factors. *Strumigenys* are not attracted to typical ant baits, they have cryptic habits such as playing dead when disturbed, they are very small (< 3mm in total length), and they have small colonies that typically nest in an area the size of a hickory nut, all of which decrease their chance of detection (Wesson 1939, Wesson and Wesson 1939, Duffield and Alpert 2011, Booher, MacGown et al. 2012). *Strumigenys* not detected by visual search or present at baiting stations are often present in litter-extractions (Delabie, Fisher et al. 2000, Lopes and Vasconcelos 2008).

Because no previous study has attempted to investigate *Strumigenys* communities, this project was a feasibility study to determine whether one could design rapid sampling methods to investigate *Strumigenys* communities. Existing ant sampling methods are labor- and time-intensive. This study developed a less labor-intensive sampling protocol than standard ant survey

protocols, one specifically optimized for sampling *Strumigenys* communities. The study also investigated *Strumigenys* ant communities on two different spatial scales.

2.2.2 Developing a new rapid sampling protocol

The Ants of the Leaf Litter (ALL) Protocol, a recently developed method for sampling ants (Agosti and Alonso 2000), relies heavily on passive litter-extraction methods and has been adopted by many biologists interested in ant diversity. This protocol method gives consistent and reliable same-site results in terms of species richness and abundances. The ALL Protocol is an improved and valuable survey method, but a major drawback is that it is too time consuming for a single investigator to use in more than a few localities in a single field season. From collection to data entry, each ALL Protocol sample site takes an estimated 161.5 hours (Agosti and Alonso 2000). However, some myrmecologists report that the time actually required per site is more than double this time estimate for the ALL Protocol per site (Agosti and Alonso 2000). In this study, I compare the time effort and results of the litter-sampling portion of the standard ALL Protocol to less intensive subsampling of the same site using modified methods tested in this study.

An additional problem with the ALL protocol is the "one sample size fits all species" assumption. The protocol only uses a scale of one square meter (taken from transects), but this size may be too large when investigating small ants and/or small colonies and too small when investigating large ants and/or large colonies. This one size fits all is particularly problematic if one is studying interactions among species in an ant community. Large ants are likely to have colonies that forage over distances of several meters, and therefore potentially interact with conspecifics from other colonies co-occurring in the same square meter. Conversely, small ants such as *Strumigenys* may never forage more than 10-50 cm away from their nest and may never interact with other colonies co-occurring even within the same square meter.

2.2.3 Repeatability of sampling results

Repeated sampling may fail to provide similar results. If communities change between repeated samples, or if the area subsampled is too small, the subsample may not estimate the actual species present at a 0.20 ha site. This is because of the species-area relationship within a site. How many species a "site" has is a function of how big it is. It is not feasible to completely sample all of the litter within a 0.20 ha, so my goal is to subsample enough area within a 0.20 ha site to obtain consistent results in terms of species richness and abundance of *Strumigenys*. As the goal is to evaluate *Strumigenys* communities and the goal of subsampling is to provide an estimate of the species at sites, I test whether repeated subsamples provide similar estimates of which species occur and how many of those species occur at a particular site. Because *Strumigenys* colonies have annual growth cycles (Duffield and Alpert 2011), sampling when colonies of *Strumigenys* have smaller colony sizes may result in a lower probability of detecting species that are actually present, especially rare species. Because the goal is to compare *Strumigenys* between sites and because results vary depending on whether colonies are larger or smaller, sampling should control for predictable annual changes in colony size. Thus sampling needs to be completed in the narrowest window of time possible. However, increasing the number of sites sampled will increase the length of time it will take to sample more sites and this time constraint must also be considered when designing a study. I tested whether samples are more likely to have more *Strumigenys* individuals and species in samples collected in July and August when colonies are largest compared to samples taken at the same site in May and June when colonies are smaller. If the anticipated seasonal changes occurred, then the plan was to examine how the seasonal changes in *Strumigenys* communities affect the repeatability of samples.

2.2.4 Winkler vs. Berlese

Several methods exist to extract litter-dwelling arthropods. Some methods, such as high gravity flotation methods and the Murphy split-funnel dry method, show bias among different arthropod groups (Petersen and Luxton 1982). A review of more than 20 extraction methods indicates that the Berlese dry funnel method is the least biased extraction method among different arthropod groups (Petersen and Luxton 1982). However, Winkler methods are favored among myrmecologists for their efficiency in extracting ants that move towards, instead of away from light, and ease of use in the field (Agosti and Alonso 2000). Berlese and Winkler methods extract arthropods by different mechanisms. Winkler sampling involves placing sifted litter into mesh bags from which insects can escape and hanging these bags inside a larger sack that can be tied shut. A vial of alcohol placed at the funneled bottom end of the Winkler bag collects specimens as they fall from the litter-filled hanging mesh bags during drying. Berlese funnels consist of a funnel capped with a lid containing a light bulb; with the sifted litter placed on a round wire mesh tray half way down the shaft of the funnel. Berlese methods, which use light bulbs to heat and dry the litter, may take as little as three hours, but extraction time relies on the moisture content and amount of litter placed in the Berlese funnel. The advantage of Winkler over Berlese extractions are their mobility and ease of use in the field. Berlese funnels are bulky and require electricity. Although many myrmecologists prefer Winkler extractions and Berlese extractions are the least biased, I chose these two methods to compare extractions of the same site to determine the most efficient method to extract *Strumigenys*.

2.2.4 Environmental variables

Temperature and precipitation influence ant diversity patterns (Kaspari, Yuan et al. 2003, Dunn, Agosti et al. 2009). As with most groups of ants, *Strumigenys* reaches its highest species

diversity in tropical wet environments (Dunn, Agosti et al. 2009). In the United States, *Strumigenys* are abundant and diverse only in moist temperate/subtropical environments of the southeast. The few US species occurring in arid regions are mostly associated with moist microenvironments such as southwestern desert species *S. arizonica* (Ward, 1998) that cohabits underground nests built by *Trachymyrmex arizonensis*. Though temperature and moisture requirements often limit species ranges (Wiens 2011) other biotic and abiotic variables may also constrain where species live (Levins and Macarthur 1966). Because little is known about *Strumigenys* habitat preferences or their physiological tolerances, I measured or characterized as many biotic and abiotic variables are known to, or are likely to, influence ant colonization and survivorship. I measured the variables listed in Methods (see also Appendix I below) in both the 0.20 ha sites and in the 1.0m^2 microsites. If sampling large 0.20 ha sites reveal *Strumigenys* are not randomly dispersed, environmental measures and habitat characteristics may inform habitat preferences. These variables may clue biotic interactions, predict physiological tolerances, and help explain community assembly *i.e.* what environments matter to which species. Further sampling at smaller scales in conjunction with environmental observations can reveal similar patterns as those in 0.20 ha sites. Interspecific trade-offs are typically thought to be a requirement for species coexistence in communities at small spatial scales (Macarthur and Pianka 1966, Tilman, Kilham et al. 1982, Wedin and Tilman 1993, Chesson and Huntly 1997). Occurrence patterns at small local spatial scales may reveal that species co-occur at random, prefer similar environments, or tend to not co-occur and thus avoid potential competitive interactions.

2.3 METHODS

2.3.1 Site description

Sandy Creek Nature Center is a nature preserve in Athens, GA and is in the upper piedmont physiographic region. In the center of Sandy Creek Nature Center is a peninsular ridge about 50 feet higher than the flood plain that surrounds it on the south, southeast, southwest, and west borders. I defined four habitats within Sandy creek and quantified these habitats by recording environmental measures and biotic characteristics at each site. Three habitats (bottomlands, flat-woods, and sloped forests) have near equal coverage around 30% and one habitat (manicured fields) makes up about 10% of total area. A few trees occupied most habitats. Dominant tree species were beech and cottonwood in bottomlands, pine and sweet gum in flat-woods, and oaks, hickories, and poplar in sloped-forest habitats.

2.3.2 Sampling Methods

I surveyed, at random, 9% of 80 hectares. Using a map, I divided Sandy Creek Nature Center into a grid of 400 evenly sized areas representing 0.20 ha each, omitting areas composed primarily of water, *e.g.* lakes and rivers. In total I omitted an additional ten 0.20 ha areas because they contained large areas covered by roads and buildings. With the gridded map labeled from east to west and north to south from 1-390, I used a random number generator (random.org) to select 36 sites by number resulting in 10.8% of numbered sites to be sampled. I sampled each site twice taking environmental measurements. Using Google Earth, I recorded and labeled each site with a latitude and longitude coordinate that corresponded to the center of each site.

I created a boundary with each of four sides equaling 45 m long (sites = 2025m^2 and termed 0.20 ha sites). I chose a subset of microsites and habitats within each 0.2 ha site. Chosen within-site samples consisted of sifted litter and organic soil from areas including, but not limited to: litter

under open and closed canopy; areas around and under structure including rocks, standing dead trees, and fallen logs and branches; and litter and soil from topographically distinct areas such as depressions, flat areas and slopes. I continued sampling until each sifted litter sample consisted of 3.75 l of sifted litter and organic debris. I attempted to sample areas within sites consistent with the abundance of ground cover estimated from transects (see Appendix I for descriptions of transects). I sampled sites in random order without replacement until I had sampled all 0.20 ha sites. I sampled each site a second time following the identical protocol of the first sample, but never sampling from the previous subset of microsites or habitats. I sampled between two and six sites per day and collected environmental data and categorical habitat data (see methods below, Appendix I, and **Tables 2.2-2.4**).

In the most diverse 0.20 ha site, site SCNC-342 (center of site was 33.98173N -83.38250W), I randomly sampled 20 one-m^2 plots to determine if species utilize different resources or environments within the larger habitats that they occupy. I collected all samples within a two-day period. I manually broke apart all small woody debris and litter and broke apart larger branches with a hatchet in each square meter sampled. I vigorously mixed and sifted all litter and woody debris from each microsite through a 1.0cm^2 wire mesh and placed sifted materials into Santos® breathable bags. Berlese funnels extracted arthropods from litter using a 25-watt bulb for two days. Extracted arthropods fell directly into vials containing 95% ethanol. I recorded the following characteristics and measurements at each microsite; location within 0.20 ha habitat, litter depth, stick count, litter volume, site description, nearest tree, size of nearest tree, distance of nearest tree, dominant vegetation, soil moisture, pH, humus depth, slope presence, aspect, slope gradient, composition of soil, percent of meter that is bare ground, covered in litter,

covered by stone, or covered by ground level plants (see Appendix I for definitions of variables and **Tables 2.5-2.6** for data).

2.3.3 Statistical Methods

I performed matched pairs Wilcoxon Signed Rank tests to test for mean and variance differences. Wilcoxon Signed Rank test does not assume normal distribution of data and is appropriate for small sample sizes. I employed non-parametric Wilcoxon tests for datasets that were either small (less than 15 observations) or non-normally distributed. I performed Wilcoxon X^2 one-way tests first to test whether one variable differed in response in multi-comparison tests before I performed each pair Wilcoxon tests. If datasets were large (> 15 observations) and normally distributed, I performed ANOVAs to test for mean and variance differences. To test discrete distributional data against predictions of random distributions, I performed Poisson goodness of fit tests. I performed all statistical analyses (means and standard deviations, Wilcoxon X^2 one-way, Wilcoxon each-pair, ANOVAs, linear regressions, and Poisson goodness-of-fit tests) using JMP® statistical software.

2.4 RESULTS

2.4.1 Sampling method results.

Both 0.20 ha subsampled sites and one-m^2 microsites provided statistically large sample sizes of species occurrences, co-occurrences, and absences to test for process driven patterns of community organization against random expectations (**Figures 2.27-2.28.**). An average of 16.36 ± SD 16.15 individuals, representing a mean of 3.3 ± SD 1.98 *Strumigenys* species, occurred in samples from each 0.20 ha site. Litter extraction produced at least one species from litter samples

in 86% of sites. From these sites, I recovered 589 *Strumigenys* individuals of 16 species (**Table 2.3.**).

The diversity and abundance of *Strumigenys* extracted from 20 microsites in 0.20 ha site SCNC-342 totaled 213 *Strumigenys* individuals of six species. One species (*S. abdita*) was not extracted in the previous habitat sampling of the same 0.20 ha site, was present in microsite sampling of SCNC-342. Microsite extractions averaged 11 *Strumigenys* individuals and two species per sample. Eighty percent of microsites contained at least one species and 75% of microsites had two or more species with a single microsite containing four species (**Table 2.6.**).

2.4.2 Winkler vs. Berlese extractions

Though no significant differences resulted between paired tests, samples with Berlese funnels extracting the largest *Strumigenys* abundances and number of *Strumigenys* species (**Table 2.1.**).

2.4.3 Repeatability of results

Repeated subsampling of the 0.20 ha sites showed that the volume of leaf litter examined in subsamples yielded good estimates of the most abundant species at a given site. Sifted litter volume in microsites averaged 3.16 l per m^2 and yields an estimate of 6,320 l of sifted litter in a 0.20 ha site. The total volume of sifted litter examined in initial and repeated sampling is 7.5 l per site, or 0.12% of the total estimated sifted litter in a 0.20 ha site. Even though the volume of litter subsampled at a site is a small fraction of the total litter, *Strumigenys* occurring in first and second subsamples were similar. In sites where litter extractions produced at least one *Strumigenys*, the same species had a probability of 0.71of being extracted a second time. Species with higher abundances in 0.20 ha sites were more likely to occur in both samples (one-way

Anova, R^2 = 0.30, n = 117, F = 48.6, p < 0.0001; **Figure 2.1**.). Although initial subsamples efficiently estimated species present in 0.20 ha sites, secondary subsampling increased species discovery by an average of more than two species (Mean 2.2, Std Dev 1.3, Std Err Mean 0.23, n = 36).

2.4.4 New rapid sampling methods vs. the ALL protocol

The time it takes to subsample 0.20 ha sites using methods described in this study is much less than the equivalent ALL Protocol methods. The litter sampling methods of the ALL protocol calls for 20 litter extractions from square meter sites randomly chosen along a transect within a specific habitat. This protocol took nearly seven times longer to complete. At SCNC-342, sampling 20 square meter plots required collecting 63.29 l of sifted litter, consumed 17 hours of fieldwork, and took 50 hours of time in the laboratory to complete. Subsampling the 0.20 ha sites twice using the less intensive subsampling methods of this study resulted in only 7.5 l of sifted litter collected, consumed 5.5 hours of fieldwork, and took 4.4 hours of lab work to complete.

Strumigenys species recovered by microsite samples and subsamples were similar, with 63% of the same species recovered by the 20 microsites sampled and subsampling methods at site SCNC-342. However, randomly sampled microsites (ALL Protocol) produced one fewer species (six) than subsampling methods of this study (seven species).

Species richness (linear regression, R^2 = 0.07, n = 72, F = 5.1, p = 0.03, **Figure 2.2**) and abundance (linear regression, R^2 = 0.08, n = 72, F = 6.3, p = 0.015, **Figure 2.3**) increased in extracted litter samples over the time-period of May through July. Even though the diversity and abundance of *Strumigenys* extracted in litter samples was highest in July, the correlation between time (number of days between same-site litter samples) and the probability of extracting the

same species in both samples was not significant (**Figure 2.4**). Same-site collections made 54-75 days apart were just as likely to capture the same species as collections made 9-29 days apart.

2.4.5 Environmental variables and *Strumigenys*

Larger 0.20 ha sites are appropriately scaled to define general habitats and determine environmental differences between habitats. Sites within the 0.2 ha areas differed in biotic characteristics and environmental measures and provided potential predicting factors to investigate *Strumigenys* communities. Characteristics of habitats (topography, site description, vegetation size, and soil description) did not vary between and were consistent first and second site characterization and reflected actual differences between 0.20 ha sites (**Table 2.2**). Environmental measures (average litter depth, pH, temperature, and soil moisture) taken at sites at two different times were similar and described differences between 0.20 ha sites (**Figures 2.5-2.9**). However, methods used to categorize percent cover (percent bare, litter, stone, and plant) of 0.20 ha sites had large variation and were not consistent between first and second estimations of characterizations of general habitat differences between sites and reveal larger within site sampling of these variables is needed to more accurately characterize habitats according to these variables (**Figures 2.10-2.13**).

Several characteristics of habitats correlated to *Strumigenys* abundance or diversity, thus revealing environmental variables likely to matter to the presence or absence of *Strumigenys*. Diversity ($X^2 = 15.70$, $p < 0.003$) and abundance ($X^2 = 13.13$, $p < 0.01$) of *Strumigenys* differed by general habitat topology, with bottomlands having lower diversities and abundances than sloped or flat forests (for each-pair Wilcoxon test $Z > 2.0$, $p < 0.05$). Abundances of *Strumigenys* differed by dominant vegetation in 0.20 ha sites (Wilcoxon $X^2 = 17.6$, $p < 0.01$) with sites having

lower abundances in sites dominated cottonwoods (*Populus deltoides*) than those dominated by *Pinus spp.* (Wilcoxon each pair, $\underline{Z} = 2.6$, $p = 0.01$). Lower abundances also occurred in primarily oak forests (*Quercus spp.*) when compared to eastern gum forests (*Liquidambar styraciflua*) (Wilcoxon each pair, $Z = 2.5$, $p = 0.02$). Diversity and abundances did not differ by sites characterized by secondary or tertiary vegetation, average tree size, or by forest type (terminology in Appendix I).

Most environmental measures of 0.20 ha sites did not predict *Strumigenys* abundance and diversity or if they did, they explained little of the variance. Variation in soil moisture, slope aspect, pH, and litter depth did not correlate with *Strumigenys* diversity. Temperature and percent ground cover were the only environmental measurements with significant correlations to *Strumigenys* diversity and/or abundance. *Strumigenys* diversity ($R^2 = 0.12$, $n = 36$, $F = 4.6$, $p = 0.04$) and abundance ($R^2 = 0.13$, $n = 36$, $F = 4.8$, $p = 0.04$) negatively correlated with increased bare ground. Litter, stone, and herbaceous plant cover had no significant relationship with diversity or abundance. Sites with cooler air (linear regression, $R^2 = 0.16$, $n = 61$, $F = 11.07$, $p = 0.0015$) and leaf litter temperatures (linear regression $R^2 = 0.16$, $n = 72$, $F = 13.45$, $p = 0.0005$) had higher *Strumigenys* abundances and species richness (linear regression air temperature and species richness, $R^2 = 0.08$, $n = 61$, $F = 5.42$, $p = 0.0234$; linear regression litter temperature and species richness, $R^2 = 0.10$, $n = 71$, $F = 7.87$, $p = 0.0065$; **Figures 2.14-2.17**). Lower soil temperatures also correlated with higher species richness ($R^2 = 0.12$, $n = 71$, $F = 9.70$, $p = 0.003$; **Figure 2.18**), and *Strumigenys* abundance ($R^2 = 0.10$, $n = 71$, $F = 7.65$, $p = 0.007$; **Figure 2.19**). Presence or steepness of slope did not explain *Strumigenys* diversity, but no *Strumigenys* occurred from samples from north facing slopes (Pearson Likelihood 7.2 $p = 0.007$), but occurred in all samples from south and southwest facing slopes. None of these correlations is at

all strong; even the strongest variables explained < 20% of the variation in diversity or abundance (R^2 values).

In 1.0m^2 microsites, species richness increased with the number of sticks present, with sticks explaining 14.4% of the species richness variance ($R^2 = 0.38$, $n = 20$, $F = 10.9$, $p = 0.004$, **Figure 2.20**). *Strumigenys* richness ($R^2 = 0.32$, $n = 20$, $F = 8.5$, $p < 0.01$), and abundance ($R^2 = 0.23$, $n = 20$, $F = 5.4$, $p < 0.04$) increased with increased litter volume m^{-2} (both litter volume and stick number are proxies for potential nesting sites) **Figures 2.21-2.22**. Though average leaf litter correlates with litter volume m^{-2} ($R^2 = 0.20$, $n = 20$, $F = 4.6$, $p < 0.05$), *Strumigenys* abundance increases more strongly as a function of litter volume ($R^2 = 0.23$, $n = 20$, $F = 5.4$, $p < 0.05$). Of the four characterized ground covers, only bare ground correlated with *Strumigenys* diversity. *Strumigenys* diversity ($R^2 = 0.41$, $n = 20$, $F = 12.3$, $p = 0.0025$) and abundance (not significant, $R^2 = 0.17$, $n = 20$, $F = 3.6$, $p < 0.07$) increased as a function of percent of bare ground within microsites.

Soil moisture content negatively correlates with pH in microsites ($R^2 = 0.72$, $n = 20$, $F = 47.3$, $p < 0.0001$, **Figure 2.23**). As *Strumigenys* abundance decreases as a function of average soil moisture content ($R^2 = 0.22$, $n = 20$, $F = 4.9$, $p = 0.04$, **Figure 2.24**), abundance ($R^2 = 0.23$, $n = 20$, $F = 5.3$, $p = 0.03$, **Figure 2.25**) and species richness ($R^2 = 0.25$, $n = 20$, F = 6.1, $p = 0.02$, **Figure 2.26**) increases as a function of average pH.

2.4.6 Distributions of *Strumigenys*

Litter sample extractions of 0.20 ha sites produced a non-normal distribution of species richness and thus did not support the null hypothesis (**Figure 2.27**). Microsite litter extractions produced the same distributional pattern of species richness as 0.20 ha habitats (**Figure 2.28**). In 0.20 sites,

more sites contained one or no species and more sites contained four or more species than expected by a Poisson distributional fit of expectation for a mean of 3.3 species per site (Goodness-of-Fit Test, Pearson X^2=41.6, p = 0.20**; Figure 2.27**). Similarly, in microsites there were more sites with no species and more sites with two or three species than expected from a Poisson distribution fit of expectation for a mean of 1.9 species per microsite (**Figure 2.28**). In both 0.20 ha sites and at microsites fewer species tended to occur in more habitats and more species tended to occur in more habitats than expected at random.

2.5 Discussion

Sampling of just 10% of all potential 0.20 ha sites of Sandy Creek Nature Center (SCNC) using rapid-sampling protocols resulted in the collection of sixteen species. This is more than two times the number of species collected in a recent statewide survey and equal to the number of *Strumigenys* reportedly collected in the entire state of Georgia, USA (Ipser, Brinkman et al. 2004). Methods described here show the abundance and diversity of *Strumigenys* in southeastern forests are much greater than previously reported and provide evidence studying *Strumigenys* communities is feasible, provided one uses rapid sampling protocols. The actual area of habitat sampled (leaf litter and woody debris) within a 0.20 ha site was a fraction of a percent of the volume of total potential nesting sites. Even so, the recovery of the same species in repeated samples and the diversity of species indicates that the new, more rapid sampling methods yield more accurate and/or more efficient extraction of *Strumigenys* than previous methods (Agosti and Alonso 2000, Ipser, Brinkman et al. 2004). Rapid sampling methods described here resulted in the same number of species extracted as methods analogous to the ALL protocol in less than 15% of the time. Even though subsampling will always result in the under-representation of rare

species, rapid sampling methods provide a higher estimate of *Strumigenys* species present when compared to other collection methods. Seventy-one percent of the species collected in one sample at a given 0.20 ha site recurred in repeat samples of the same site. The number of species collected with the rapid sampling method at SCNC is equal to all previously known collections from the entire sate of Georgia, USA. This suggests that rapid sampling is the best currently available method for estimating not only the number of species in a site, but also for estimating abundances of common species at a site. These results confirm that the study of *Strumigenys* communities is feasible.

Though most variables had low explanations of the variance of *Strumigenys* abundance and species richness, many were none-the-less significant and likely important. These results support rejection of the null hypothesis that *Strumigenys* ant species have no environmental preferences and equally inhabit all sites and habitats. Many environmental variables and habitat characteristics showed environmental under-dispersion or over-dispersion of *Strumigenys* within 0.20 ha sites and 1.0m^2 microsites. In 0.20 ha areas *Strumigenys* were positively associated with forested habitats that were neither floodplains nor ridges, suggesting that flood disturbance (colonization) and moisture (desiccation resistance) might limit *Strumigenys* distributions to specific environments. More *Strumigenys* species also occurred in cooler sites, which is interesting because no *Strumigenys* were extracted from north facing 0.20 ha sites. It is likely that measures of temperature correlated negatively to insolation, which might be an important variable to measure in future studies. At the smaller 1.0m^2 spatial scale, more *Strumigenys* occurred in non-bare ground microsites with more leaf litter, and more sticks. This suggests most *Strumigenys* have similar nesting requirements. Inconsistencies in measurements of some variables, namely percent ground cover, could have large effects on results and conclusions of

whether *Strumigenys* had true associations to those measured variables or not. Future studies would need to increase the number of environmental measurements taken for each variable at each site to determine a better estimated level of significance between *Strumigenys* and their environment.

Distributions of the number of species present in 0.20 ha sites or 1.0m^2 microsites are not random. The distribution of species richness in sites is bimodal, with too many microsites with fewer species than the mean, and too many microsites with more species than the mean, compared to the unimodal Poisson. This result suggests that habitats filter species at both geographic scales. Also the scale of 1.0m^2 may be still too large to assess potential biotic interactions between *Strumigenys* species. Colonies of *Strumigenys* may not interact even within a square meter because mature colonies are often confined to a single acorn or small rotten twig, from which workers forage only a few tens of cm. Thus, smaller spatial scales may be required to investigate co-occurrence patterns of *Strumigenys* and whether these co-occurrence patterns are influenced by species interactions.

2.6 CONCLUSIONS

Strumigenys occur more often in similar 0.20 and 1.0m^2 sites supporting the hypothesis that habitats filter *Strumigenys* at both scales and thus rejecting the null hypothesis that *Strumigenys* ant species have no environmental preferences and equally inhabit all sites and habitats. However, environmental variables that explain habitat filtering of *Strumigenys* differ according to spatial scale. New rapid sampling methods are less time intensive and more efficient at recovering *Strumigenys* making the study of *Strumigenys* communities feasible. However, some environmental measurements are inconsistent and additional measurements within 0.20 ha sites

will be necessary to determine the value of inconsistent variables to explaining *Strumigenys* communities. Both 0.20 ha sites and $1.0m^2$ microsites are appropriate spatial scales for investigating *Strumigenys* communities. Larger scales will need to be examined to understand how climates affect the distributions of *Strumigenys* and smaller spatial scale studies are needed in order to reveal potential biotic interactions that may be important to *Strumigenys* community assembly.

2.7 List of Figures

Figure 2.1. Species with higher abundances in sites had higher probabilities of occurring in both 0.20 ha subsamples. Species with higher abundances in sites had higher probabilities of occurring in both 0.20 ha subsamples. Species occurring once of two samples (0) in a 0.20 ha litter subsample had lower abundances than species extracted from both samples (y), $R^2 = 0.30$, n = 117, $F = 48.6$, $p < 0.0001$.

Figure 2.2 *Strumigenys* Abundance by Date Collected. Abundance of *Strumigenys* increases in litter extractions from late Spring through Summer when colonies are increasing colonies, $R^2 = 0.07$, n=72, $F = 5.1$, $p = 0.03$.

Figure 2.3 *Strumigenys* Richness by Date Collected. Species richness of *Strumigenys* in litter extractions from late Spring through Summer when colonies are increasing colonies. $R^2 = 0.08$, n=72, $F = 6.3$, $p = 0.015$

Figure 2.4 Days Between Subsamples by the Probability of Extracting a Species in Both 0.20 ha Subsamples. There is no relationship between the number of days that pass between 0.20 ha site subsampling events and the likelihood of picking up the same species in both samples.

Figure 2.5 Average litter depth (mm) measured in the first 0.20 ha subsample compared to the average litter depth of the second 0.20 subsample Average litter depths of four measurements accurately characterizes 0.20 ha sites. Measurements taken during the first subsampling event correlate with secondary subsampling event measurements. R^2=0.46, n = 19, $F = 14.3$, $p = 0.002$.

Figure 2.6 Average pH measured in the first 0.20 ha subsample compared to the average pH of the second 0.20 subsample. Average pH of four measurements accurately characterizes 0.20 ha sites. Measurements taken during the first subsampling event correlate with secondary subsampling event measurements. $R^2 = 0.21$, $n = 19$, $F = 4.6$, $p < 0.05$

Figure 2.7 Average soil moisture measured in the first 0.20 ha subsample compared to the average soil moisture of the second 0.20 subsample. Average soil moisture of four measurements accurately characterizes 0.20 ha sites. Measurements taken during the first subsampling event correlate with secondary subsampling event measurements. $R^2 = 0.65$, $n = 36$, $F = 62.3$, $p < 0.0001$

Figure 2.8 Average air temperature (C) measured in the first 0.20 ha subsample compared to the average air temperature of the second 0.20 subsample. The difference between the daily average temperature in Athens Georgia and the air temperature at a site accurately characterizes 0.20 ha sites. Measurements taken during the first subsampling event correlate with secondary subsampling event measurements. $R^2 = 0.16$, $n = 25$, $F = 4.33$, $p < 0.05$.

Figure 2.9 Average litter temperature (C) measured in the first 0.20 ha subsample compared to the average litter temperature of the second 0.20 subsample. The difference between the daily average temperature in Athens Georgia and the air temperature at a site accurately characterizes 0.20 ha sites. Measurements taken during the first subsampling event correlate with secondary subsampling event measurements. $R^2 = 0.11$, $n = 36$, $F = 4.1$, $p = 0.05$

Figures 2.10

Percent ground cover of one of four categories (%Bare, T=1) measured in the first 0.20 ha subsample compared to percent ground cover of one of four categories (%Bare, T=2) measured in the second 0.20 subsample. Percent cover of %Bare in 0.20 ha sites do not accurately categorize sites. There was no significant correlation between first and second measurements taken at subsampling events. $n = 12$

Figure 2.11

Percent ground cover of one of four categories (%Litter, T=1) measured in the first 0.20 ha subsample compared to percent ground cover of one of four categories (%Litter, T=2) measured in the second 0.20 subsample. Percent cover of %Litter in 0.20 ha sites do not accurately categorize sites. There was no significant correlation between first and second measurements taken at subsampling events. $n = 12$

Figure 2.12

Percent ground cover of one of four categories (%Stone, T=1) measured in the first 0.20 ha subsample compared to percent ground cover of one of four categories (%Stone, T=2) measured in the second 0.20 subsample. Percent cover of %Stone in 0.20 ha sites do not accurately categorize sites. There was no significant correlation between first and second measurements taken at subsampling events. $n = 12$

Figure 2.13

Percent ground cover of one of four categories (%Plant, T=1) measured in the first 0.20 ha subsample compared to percent ground cover of one of four categories (%Plant, T=2) measured in the second 0.20 subsample. Percent cover of %Plant in 0.20 ha sites do not accurately categorize sites. There was no significant correlation between first and second measurements taken at subsampling events. $n = 12$.

Figure 2.14

Air temperature of 0.20 ha sites by *Strumigenys* abundance. The difference between the daily average temperature in Athens Georgia and the air temperature at a site predicts higher *Strumigenys* abundance in cooler SCNC sites. $R^2 = 0.16$, $n = 61$, $F = 11.07$, $p = 0.0015$.

Figure 2.15

Litter temperature of 0.20 ha sites by *Strumigenys* abundance. The difference between the daily average temperature in Athens Georgia and the litter temperature at a site predicts higher *Strumigenys* abundance in cooler SCNC sites. $R^2 = 0.16$, $n = 72$, $F = 13.45$, $p = 0.0005$.

Figure 2.16

Air temperature of 0.20 ha sites by *Strumigenys* richness. The difference between the daily average temperature in Athens Georgia and the air temperature at a site predicts *Strumigenys* species prefer cooler SCNC sites. $R^2 = 0.08$, $n = 61$, $F = 5.42$, $p = 0.0234$.

Figure 2.17

Litter temperature of 0.20 ha sites by *Strumigenys* richness. The difference between the daily average temperature in Athens Georgia and the soil temperature at a site predicts *Strumigenys* species prefer cooler SCNC sites. $R^2 = 0.10$, $n = 71$, $F = 7.87$, $p = 0.0065$.

Figure 2.18

Soil temperature of 0.20 ha sites by *Strumigenys* richness. The difference between the daily average temperature in Athens Georgia and the soil temperature at a site predicts *Strumigenys* species prefer cooler SCNC sites. $R^2 = 0.12$, $n = 71$, $F = 9.70$, $p = 0.003$.

Figure 2.19

Soil temperature of 0.20 ha Sites by *Strumigenys* abundance. The difference between the daily average temperature in Athens Georgia and the soil temperature at a site predicts higher *Strumigenys* abundance in cooler SCNC sites. $R^2 = 0.10$, $n = 71$, $F = 7.65$, $p = 0.007$.

Figure 2.20

Strumigenys richness by number of sticks in a one-m^2 microsite. More species occur in microsites with more sticks. *Strumigenys* often nest in empty cavities in sticks, nuts, and layers between leaf litter. Sticks represent potential nesting sites. $R^2 = 0.38$, $n = 20$, $F = 10.9$, $p = 0.004$.

Figure 2.21

Strumigenys richness by volume of sifted litter from a one-m^2 microsite. More species occur in microsites with more leaf litter. *Strumigenys* often nest in empty cavities in sticks, nuts, and layers between leaf litter. Litter volume represent potential nesting sites. $R^2 = 0.32$, $n = 20$, $F = 8.5$, $p < 0.01$.

Figure 2.22

Strumigenys richness by volume of sifted litter from a one-m^2 microsite. More individual *Strumigenys* occur in microsites with more leaf litter.

$R^2 = 0.23$, $n = 20$, $F = 5.4$, $p < 0.04$.

Figure 2.23

pH by average soil moisture in a one-m^2 microsite. pH negatively correlates with soil moisture in microsites. Sites become more anoxic and more acidic in more moist sites where water saturation reduces air exchange between the soil and air as organic detritus decomposes.

$R^2 = 0.72$, $n = 20$, $F = 47.3$, $p < 0.0001$.

Figure 2.24

Strumigenys abundance by average soil moisture in one-m^2 microsites. *Strumigenys* abundance decreases as a function of soil moisture. $R^2 = 0.22$, $n = 20$, $F = 4.9$, $p = 0.04$.

Figure 2.25

Strumigenys abundance by average pH in one-m^2 microsites. *Strumigenys* increases as a function of pH. $R^2 = 0.23$, $n = 20$, $F = 5.3$, $p = 0.03$.

Figure 2.26

Strumigenys richness by average pH in one-m^2 microsites. More *Strumigenys* species prefer soils with a pH near 7. $R^2 = 0.25$, $n = 20$, $F = 6.1$, $p = 0.02$.

Figure 2.27

Strumigenys Species Richness of 0.20 ha Habitat Sites. Four or more species occur in 0.20 ha sites than expected and more sites have zero or one species than expected by a null Poisson distribution. Mean 3.3, Std Dev 2.0, Std Err Mean 0.33, Upper 95% Mean 4.0, Lower 95% Mean 2.6, $n = 36$. Goodness-of-Fit Test, Pearson X^2=41.6, p=0.20, null hypothesis is the probability distributional data fit random expectations, the null hypothesis is rejected.

Figure 2.28

Strumigenys Species Richness of Square Meter Microsites. Two or more species occur in 0.20 ha sites than expected and more sites have no species than expected by a null Poisson distribution. Mean 1.9, Std Dev 1.2, Std Err Mean 0.26, Upper 95% Mean 2.4, Lower 95% Mean 1.4, $n = 20$. Goodness-of-Fit Test, Kolmogorov's D=0.18, p=0.19, null hypothesis is the probability distributional data fit random expectations, the null hypothesis is rejected.

2.8 List of Tables

Table 2.1 Table of Berlese vs. Winker leaf-litter extractions. Statistical comparisons using Wilcoxon signed rank test of matched pairs between Winkler and Berlese extractions show no significant differences between abundance and species richness of *Strumigenys* by extraction method.

Table 2.2

Table of Environmental Measures and Extraction Method. Sample code refers to Sandy Creek Nature Center (SCNC) for each sample (a or b). Site is the SCNC site sampled. TempA = Averaged temperature of the air at one meter. Temp L = Averaged temperature of the exposed ground surface. TempS = Averaged temperature of the soil below leaf litter or top ground cover. SM = Soil Moisture. Lit 1-4 = four measurements of Litter depth. % measures = estimated ground cover of the ground covered by bare surface, leaf litter, stone, or plants.

Table 2.3

Table of species occurrences and abundances in each 0.20 ha sites sampled at Sandy Creek Nature Center.

Table 2.4

Habitat characteristics for 0.20 ha sites. Location, elevation = El., dominant and secondary topography (Topography 1 & 2), forest types are listed by primary and secondary forest types if secondary forest type was present (MFF = mixed forest and field, MPH = mixed pine hardwood, MHP = mixed hardwood pine, MHW = mixed hardwood, HWF = hardwood forest, F = field, PF

= pine forest), Veg. size = categorical variable of relative tree size dominating each site. Veg. 1-3 = dominant, secondary, and tertiary vegetations, Soil Description = dominant soil composition, Sl Dir. = slope direction, Sl. Min and Sl. Max = minimum and maximum slope in degrees.

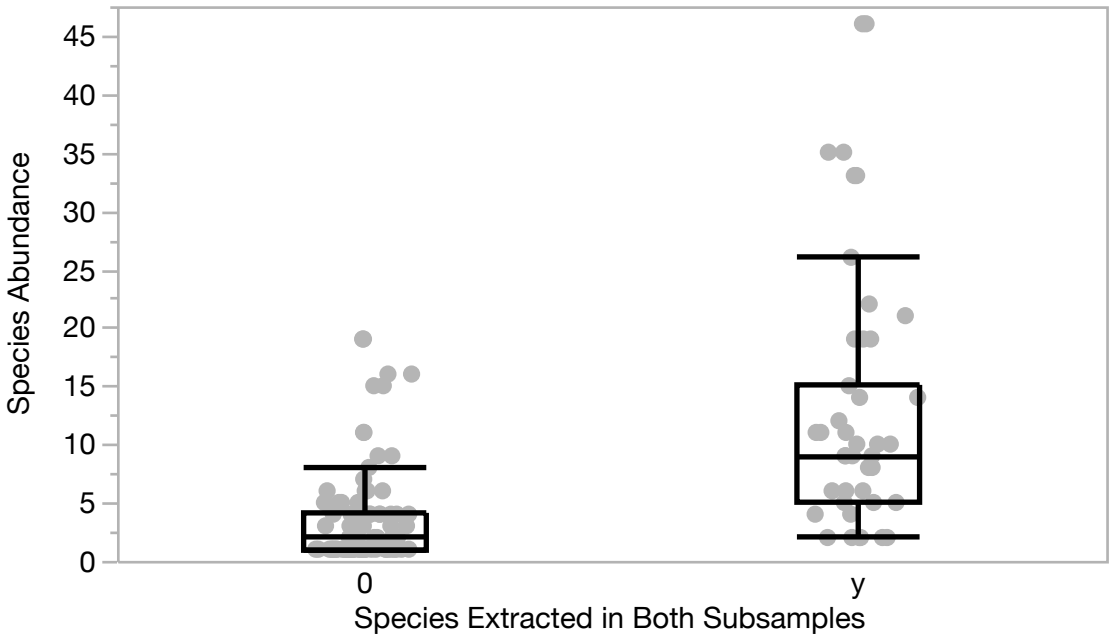
Table 2.5

Microsites characteristics. Site description = dominate topographical and vegetation description, DBH = size of nearest tree measured by DBH, m = distance in meters between microsite and nearest tree, Veg. 1 is dominant vegetation, ave L is the average leaf litter depth, n sticks is the total number of sticks present, vol L is the volume of leaf litter present, SM Ave. = average soil moisture, Humus = the the average depth of humus layer.

Table 2.6 Strumigenys abundance in microsites. Table of species occurrences and abundances in each 1.0m microsite sampled at Sandy Creek Nature Center site 342.

2.9 Figures and Tables

Figure 2.1



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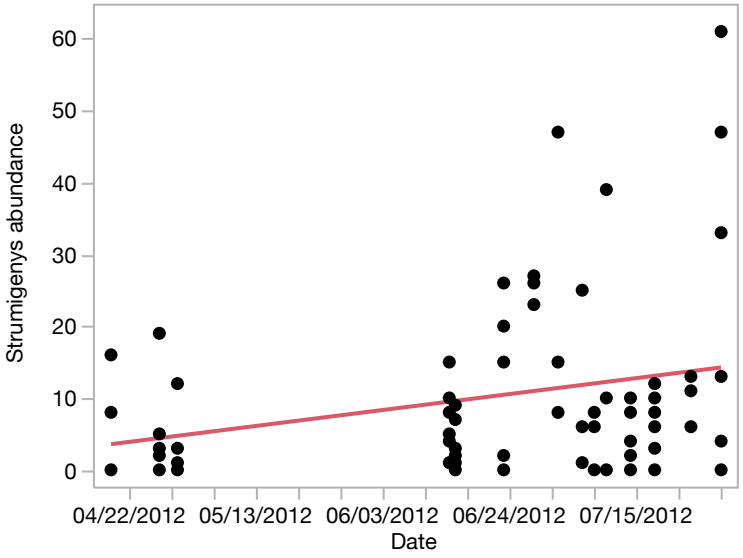

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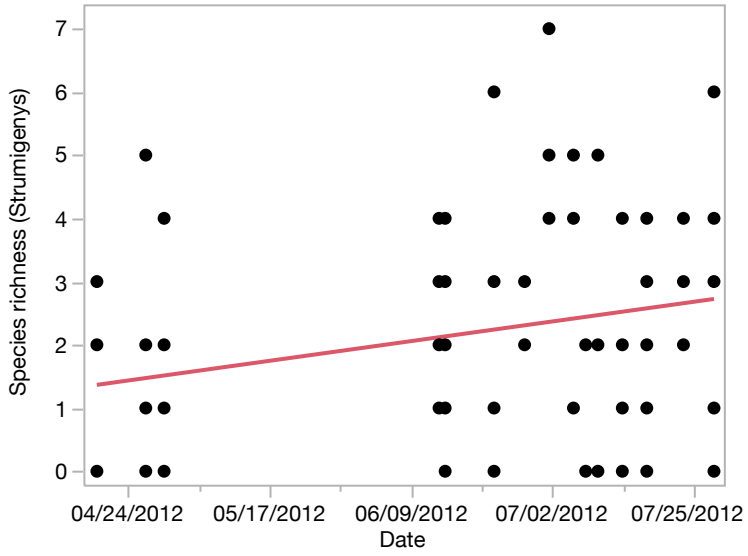

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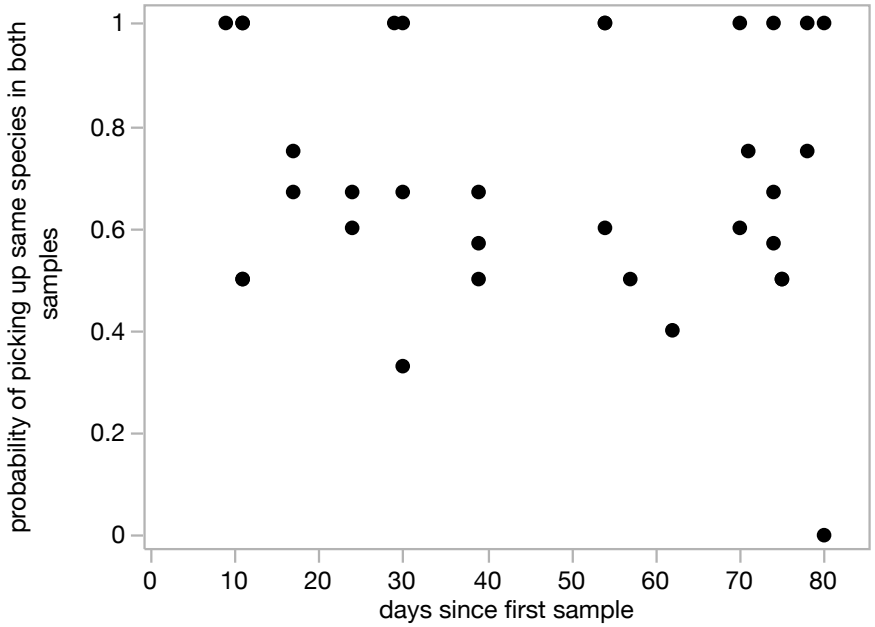

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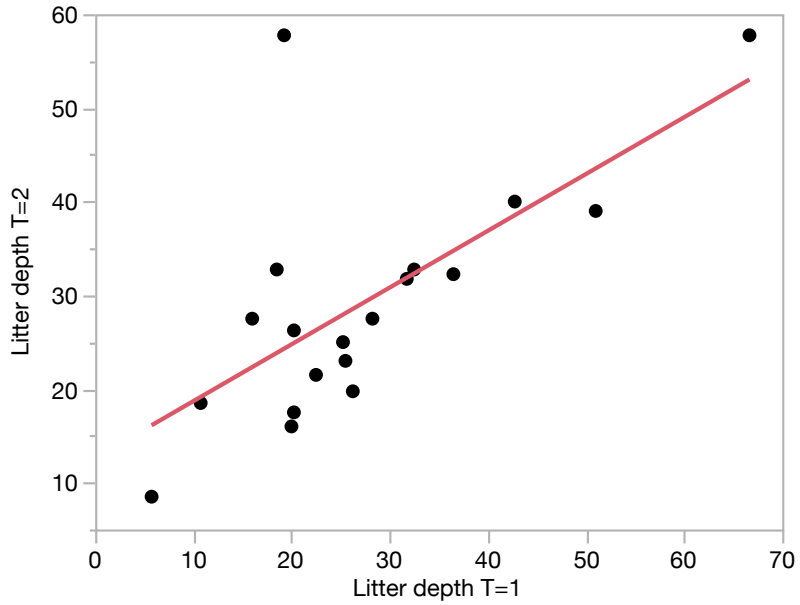

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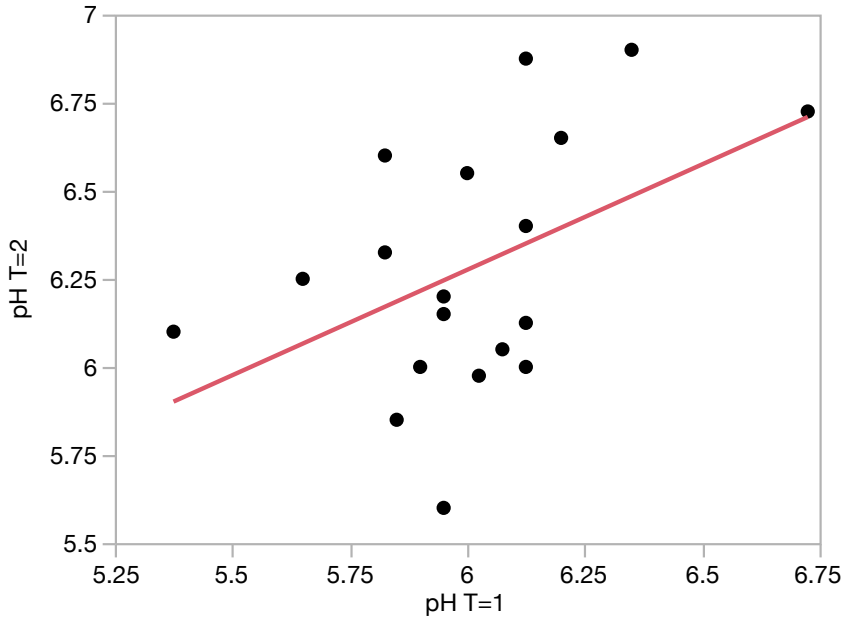

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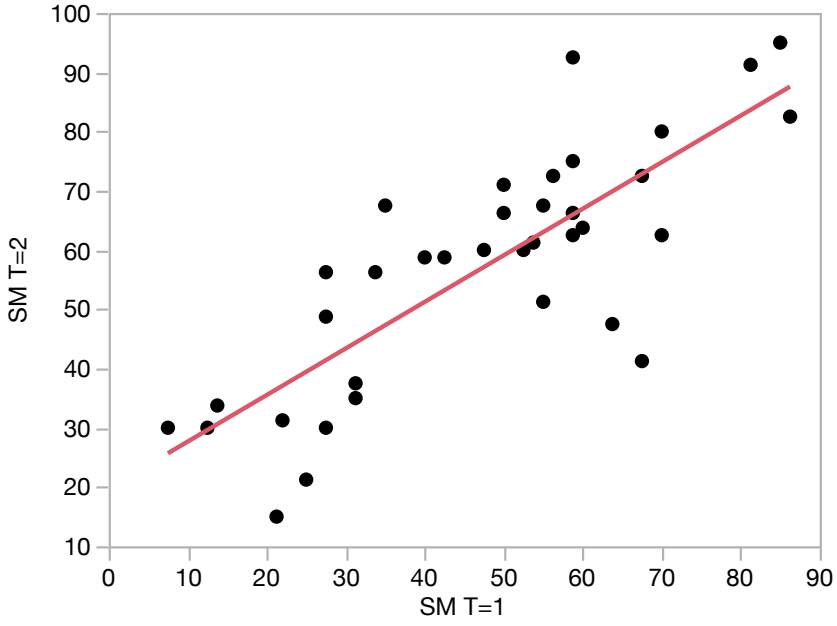

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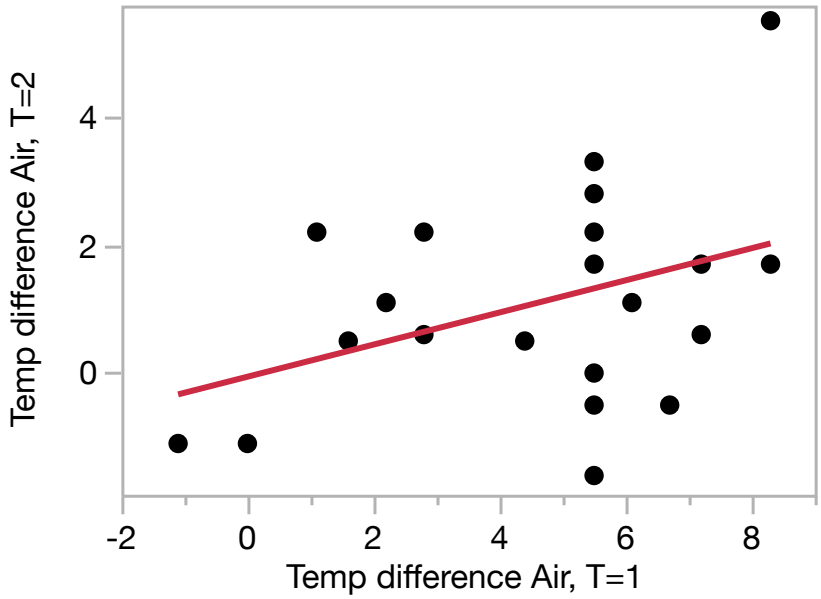

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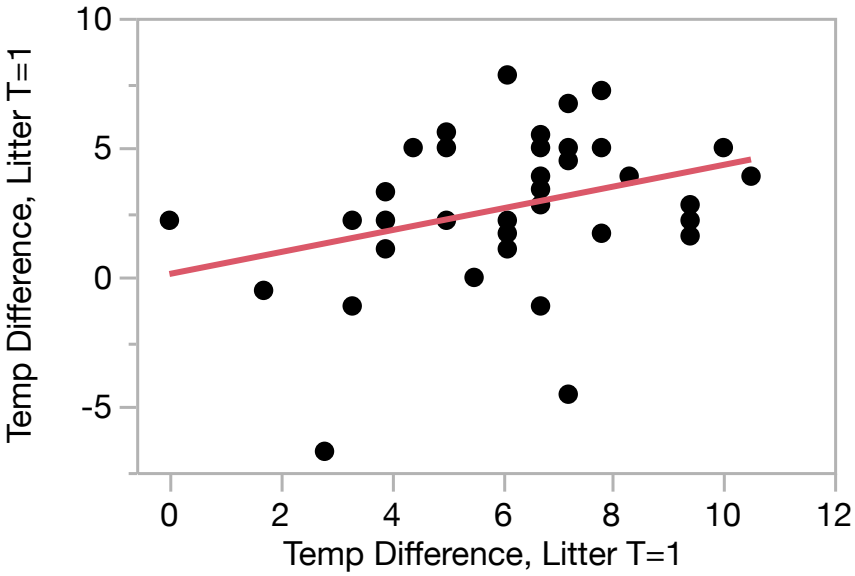

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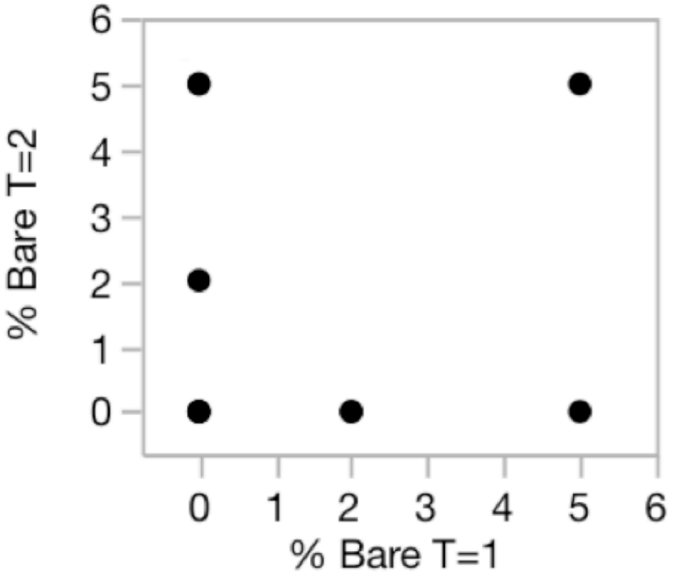

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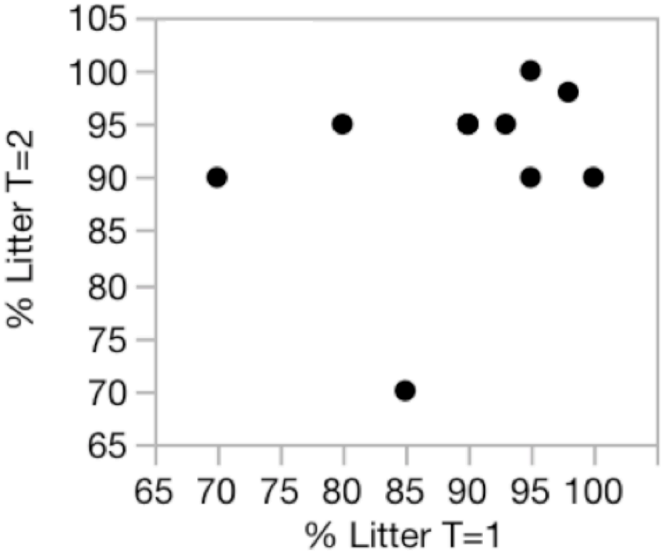

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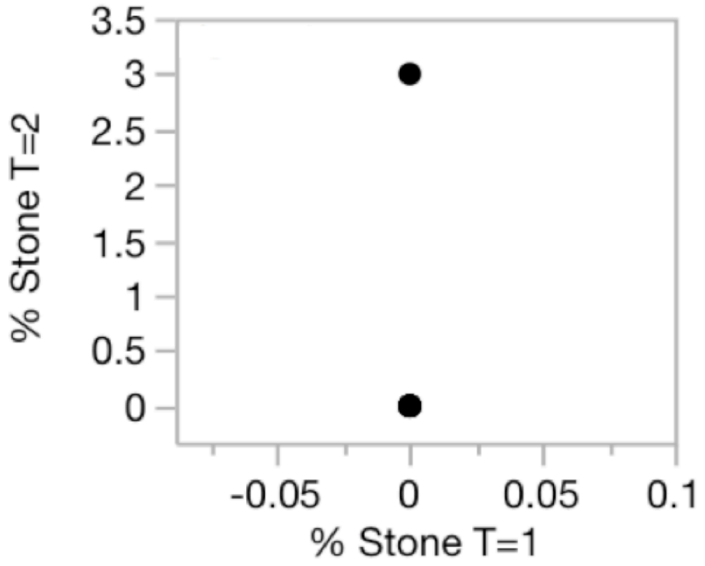

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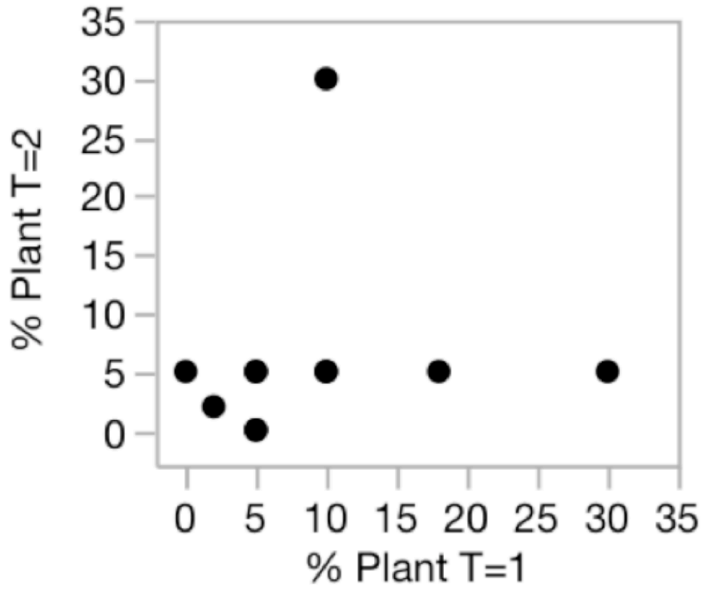

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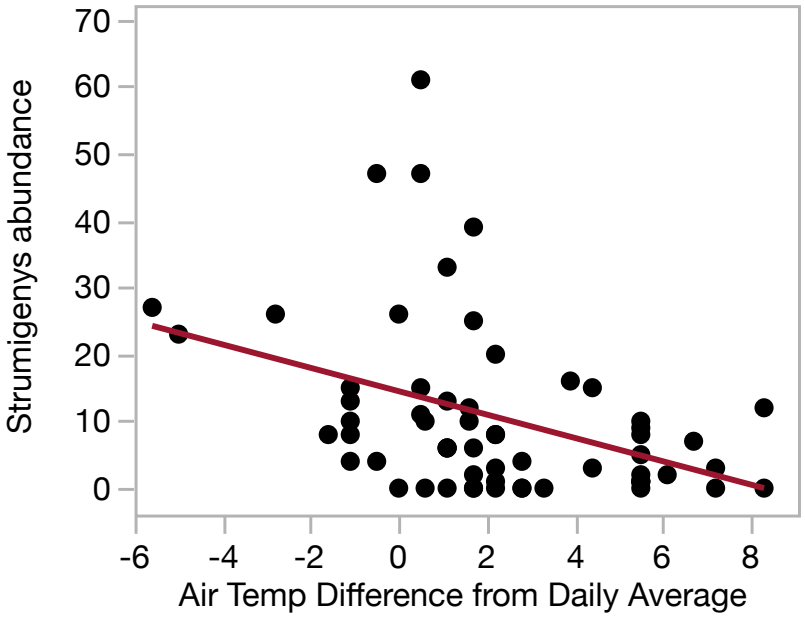

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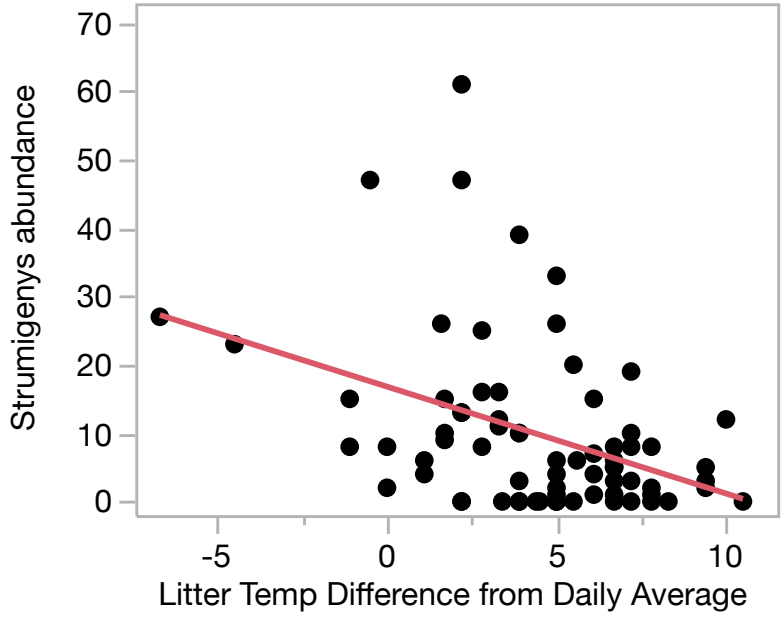

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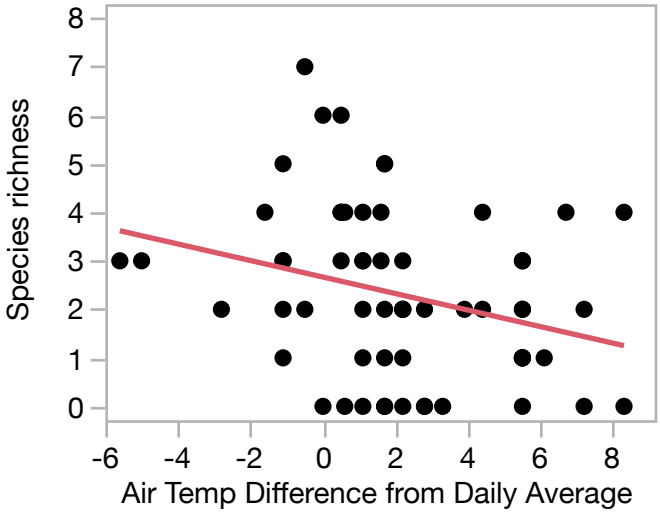

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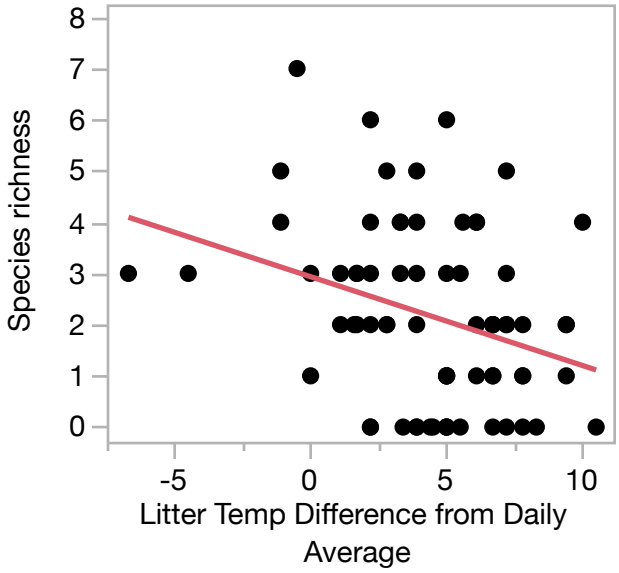

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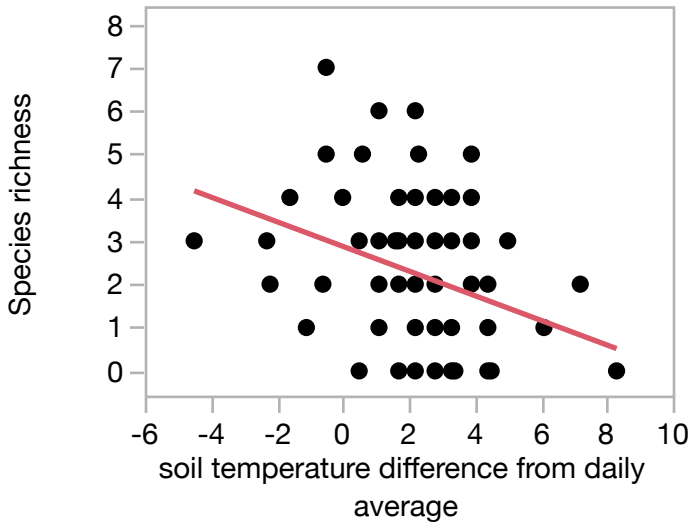

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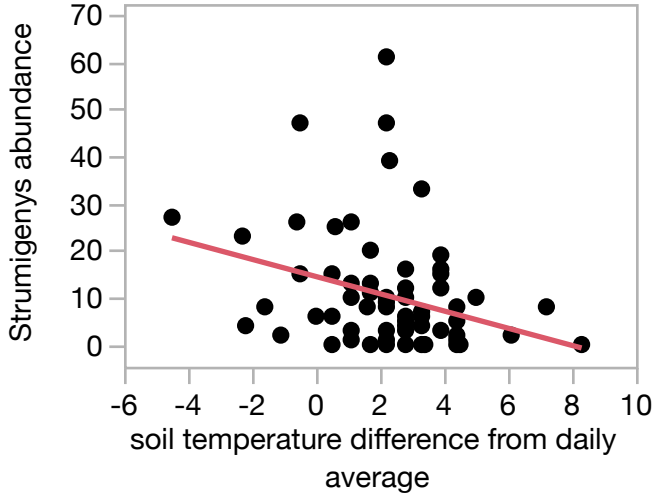

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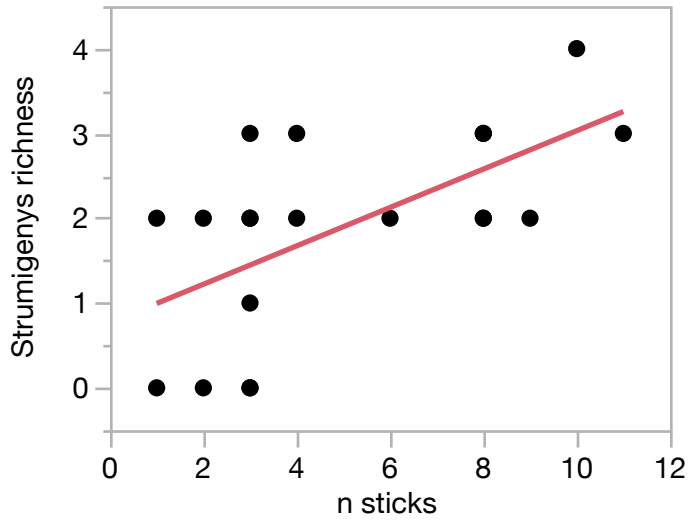

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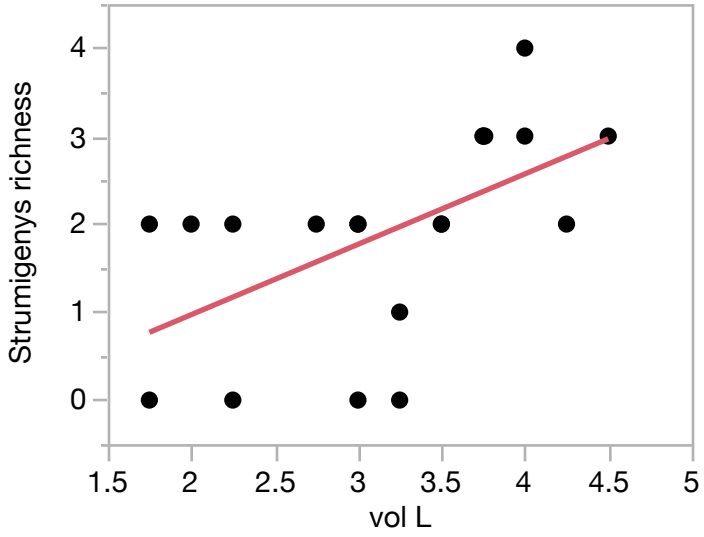

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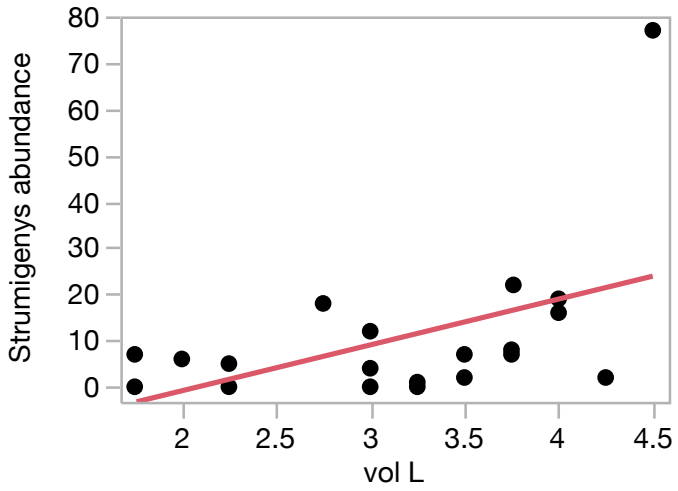

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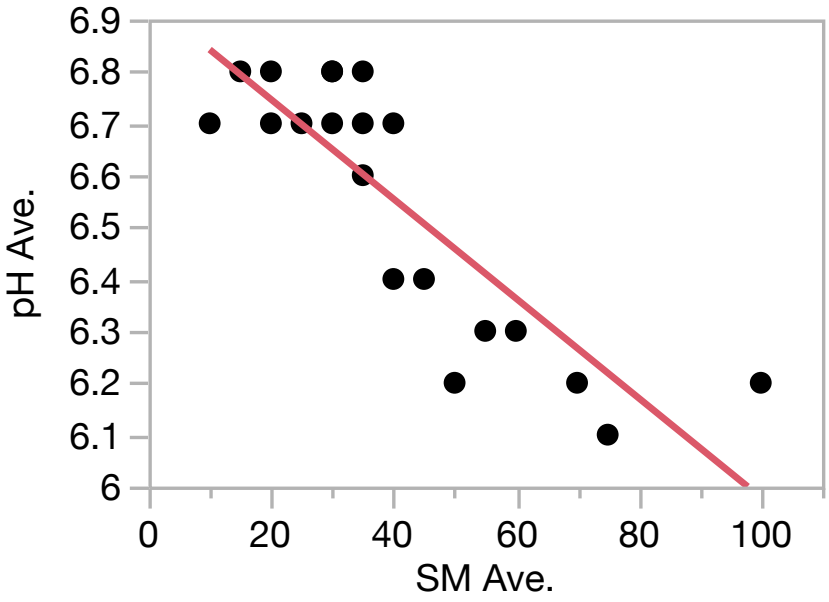

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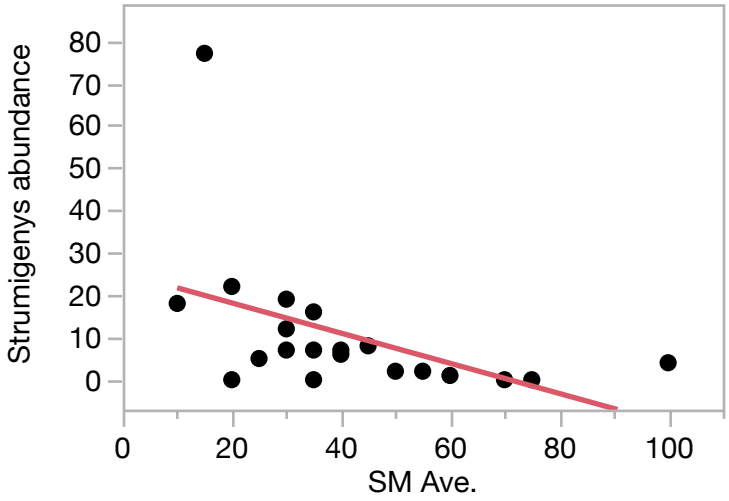

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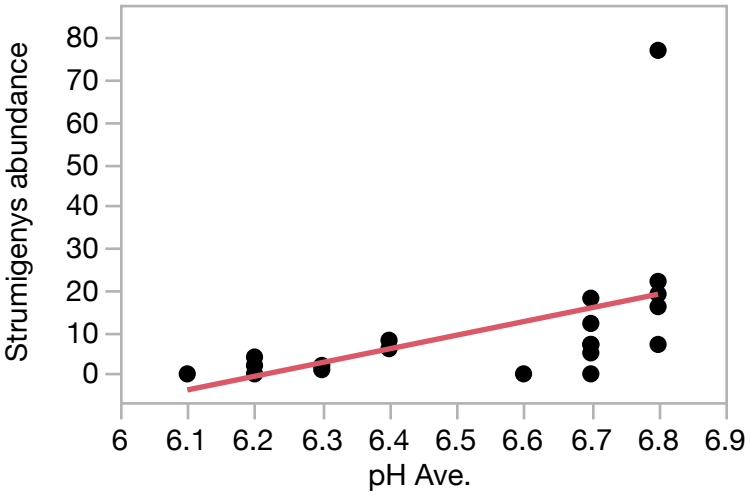
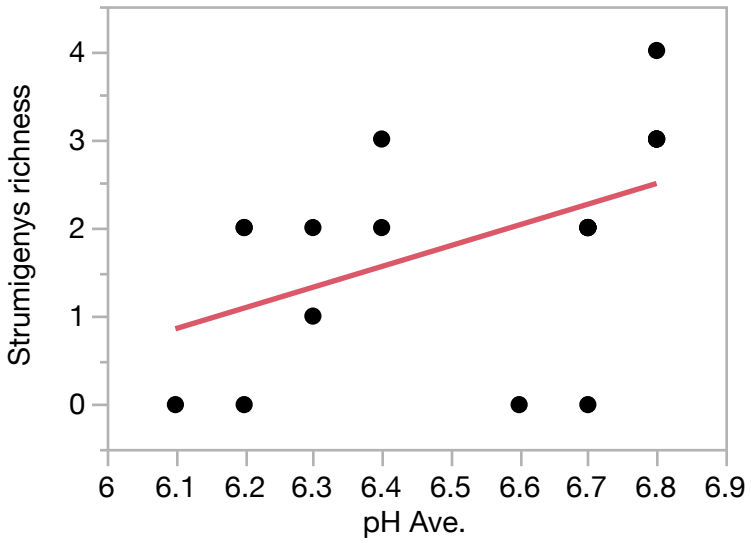


Figure 2.26



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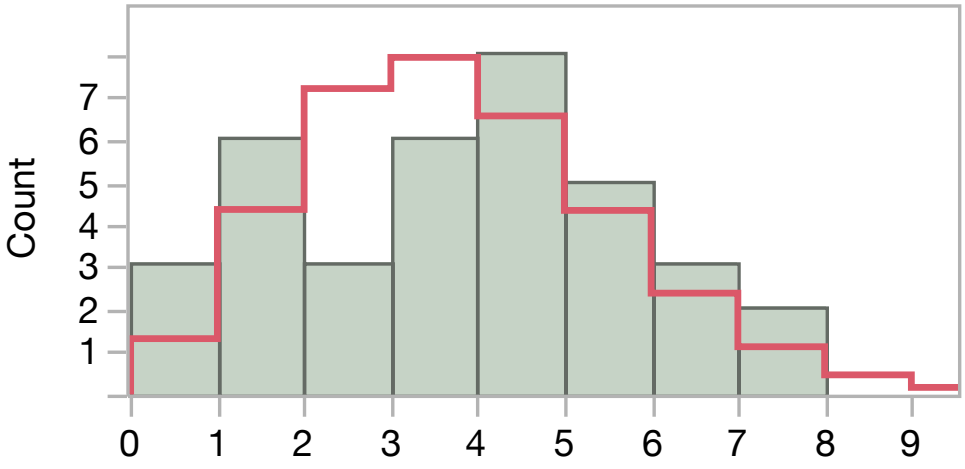

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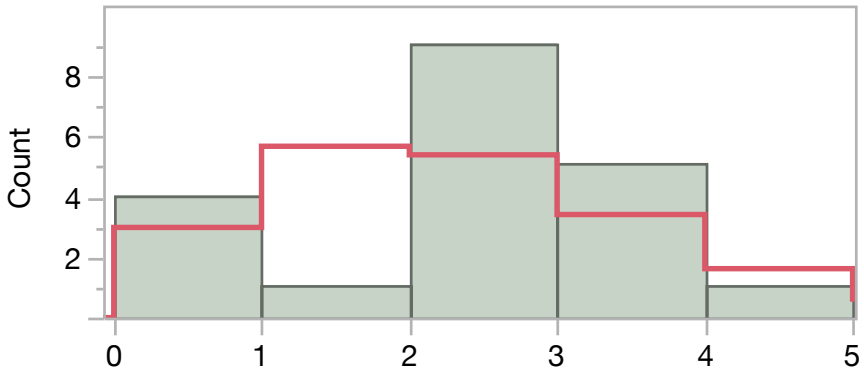

Table 2.1

Wilcoxon Signed Rank Test of Matched Pairs	Berlese Mean ± SD	Winkler Mean ± SD	prob. Berlese > Winkler	prob. Berlese < Winkler	prob. no difference	n pairs
Strumigenys Abundance	11.3 ± 2.4	8.1 ± 2.4	0.82	0.08	0.37	15
Strumigenys Diversity	2.4 ± 0.4	1.8 ± 0.4	0.84	0.17	0.33	15
Ant Diversity	8.7 ± 0.5	8.7 ± 0.5	0.46	0.54	0.9	15
Ant Biomass	10.0 ± 1.32	10.2 ± 1.32	0.51	0.49	0.98	15

Table 2.2 (page 1 of 4)

Sample Code	Site	Extraction	Date	TempA	TempL	TempS	SM1	SM2	SM3	SM4
SCNC370a	370	Berlese	4/30/12	7.2	6.7	2.8	80	35	35	40
SCNC370b	370	Berlese	7/14/12	0.6	3.9	2.2	75	75	55	50
SCNC351a	351	Winkler	4/27/12		7.8	6.1	35	40	10	35
SCNC351b	351	Berlese	7/10/12	-1.1	1.7	1.1	10	5	10	5
SCNC348a	348	Winkler	4/30/12	7.2	7.8	3.3	20	20	10	10
SCNC348b	348	Berlese	7/10/12	1.7	5.0	3.4	15	20	30	20
SCNC346a	346	Berlese	6/14/12	5.5	6.7	4.4	90	100	75	65
SCNC346b	346	Berlese	7/14/12	2.2	2.8	2.2	70	80	95	100
SCNC342a	342	Berlese	7/18/12	1.6	3.3	2.8	100	100	80	90
SCNC342b	342	Berlese	7/29/12	0.5	2.2	2.2	55	60	55	65
SCNC334a	334	Berlese	6/15/12	2.8	6.7	4.4	60	90	80	90
SCNC334b	334	Berlese	7/14/12	0.6	3.4	3.4	55	80	60	85
SCNC329a	329	Berlese	6/14/12	5.5	7.2	5.0	75	90	40	50
SCNC329b	329	Berlese	7/14/12	2.8	4.5	4.5	60	80	60	40
SCNC321a	321	Berlese	7/18/12	0.0	4.4	2.2	45	30	30	20
SCNC321b	321	Berlese	7/29/12	-1.1	5.0	3.3	13	45	15	15
SCNC319a	319	Berlese	7/18/12	2.2	7.2	1.1	55	55	55	30
SCNC319b	319	Berlese	7/29/12	1.1	5.0	3.3	30	20	30	30
SCNC313a	313	Berlese	4/19/12		7.2	7.2	55	40	20	35
SCNC313b	313	Berlese	7/8/12	1.7	6.7	2.8	15	35	50	25
SCNC302a	302	Berlese	6/15/12	6.7	6.1	3.3	60	70	55	80
SCNC302b	302	Berlese	7/14/12	-0.5	1.1	-2.2	75	60	70	30
SCNC295a	295	Berlese	4/19/12		8.3	8.3	100	90	65	35
SCNC295b	295	Berlese	7/8/12	1.1	3.9	1.7	70	80	20	55
SCNC291a	291	Winkler	4/19/12		5.0	4.5	85	70	80	5
SCNC291b	291	Berlese	7/6/12	2.2	5.0	1.1	45	45	45	55
SCNC280a	280	Berlese	6/14/12	2.8	6.1	2.8	40	35	25	35
SCNC280b	280	Berlese	7/8/12	2.2	7.8	2.2	15	10	10	20
SCNC274a	274	Berlese	4/30/12	5.5	5.5	2.8	60	60	70	60
SCNC274b	274	Berlese	6/23/12	1.7	0.0	-1.1	80	80	40	80
SCNC258a	258	Berlese	4/30/12	8.3	10.0	3.9	50	20	60	35
SCNC258b	258	Berlese	7/14/12	5.5	5.0	4.4	70	75	60	65
SCNC256a	256	Winkler	4/19/12		5.0	4.5	40	30	30	20
SCNC256b	256	Berlese	7/6/12	1.1	5.6		10	10	20	10
SCNC241a	241	Winkler	4/30/12	8.3	10.5	4.4	10	10	35	30
SCNC241b	241	Berlese	7/10/12	1.7	3.9	2.3	25	30	20	25
SCNC238a	238	Winkler	6/14/12	4.4	6.1	3.9	45	70	80	75
SCNC238b	238	Berlese	6/23/12	0.5	1.7	0.5	25	25	30	60
SCNC234a	234	Winkler	4/30/12	5.5	6.1	2.2	55	70	80	60
SCNC234b	234	Berlese	6/23/12	1.7	2.2	0.5	50	55	40	55

Table 2.2 (page 2 of 4)

Sample Code	Site	Extraction	Date	TempA	TempL	TempS	SM1	SM2	SM3	SM4
SCNC209a	209	Berlese	7/18/12	-1.1	0.0	1.6	80	70	55	30
SCNC209b	209	Berlese	7/29/12	-1.1	2.2	1.1	65	50	35	20
SCNC199a	199	Berlese	7/18/12	1.1	5.0	3.3	80	100	100	100
SCNC199b	199	Berlese	7/29/12	2.2	2.2	2.2	85	90	85	80
SCNC198a	198	Berlese	6/15/12	6.1	9.4	6.1	95	70	65	70
SCNC198b	198	Berlese	7/24/12	1.1	2.2	1.7	65	40	30	100
SCNC187a	187	Berlese	6/14/12	5.5	6.7	4.4	70	70	55	55
SCNC187b	187	Winkler	6/23/12	0.0	5.0	1.1	50	60	60	65
SCNC181a	181	Berlese	4/27/12		3.9	2.8	85	80	100	100
SCNC181b	181	Berlese	7/24/12	1.1	1.1	0.5	95	70	90	70
SCNC161a	161	Winkler	4/27/12		9.4	3.9	55	60	55	55
SCNC161b	161	Berlese	7/6/12	1.7	2.8	0.6	30	35	40	30
SCNC158a	158	Berlese	4/27/12		6.7	2.8	55	50	50	50
SCNC158b	158	Winkler	6/23/12	2.2	5.5	1.7	50	55	65	50
SCNC150a	150	Berlese	6/15/12	4.4	3.9	2.2	95	70	30	40
SCNC150b	150	Berlese	7/24/12	0.5	3.3	1.7	35	45	70	10
SCNC136a	136	Winkler	6/14/12	5.5	7.8	0.0	70	75	60	40
SCNC136b	136	Berlese	6/23/12	3.3	7.2	2.2	50	55	55	55
SCNC123a	123	Berlese	6/15/12	5.5	6.7	4.4	50	55	60	60
SCNC123b	123	Berlese	7/2/12	-1.6	-1.1	-1.6	15	30	35	30
SCNC96a	96	Berlese	6/15/12	5.5	1.7	2.2	40	70	70	60
SCNC96b	96	Berlese	7/2/12	-0.5	-0.5	-0.5	40	55	65	50
SCNC82a	82	Berlese	7/18/12	1.6	3.9	2.8	80	65	55	70
SCNC82b	82	Berlese	7/29/12	0.5	2.2	2.2	50	50	70	50
SCNC59a	59	Winkler	4/19/12		3.3	3.9	90	60	70	70
SCNC59b	59	Berlese	7/2/12	-1.1	-1.1	-0.5	70	70	80	50
SCNC38a	38	Winkler	4/27/12		9.4	2.8	35	30	35	20
SCNC38b	38	Berlese	6/28/12	-2.8	1.6	-0.6	35	20	25	30
SCNC19a	19	Berlese	4/19/12	3.9	2.8	2.8	58	70	78	78
SCNC19b	19	Winkler	6/28/12	-5.6	-6.7	-4.5	50	55	45	50
SCNC16a	16	Berlese	4/27/12		7.2	3.9	40	35	30	35
SCNC16b	16	Winkler	6/28/12	-5.0	-4.5	-2.3	30	40	30	25

Table 2.2 (page 3 of 4)

Sample Code	pH	pH	pH	pH	Lit 1	Lit 2	Lit3	Lit4	% Bare	% Lit	% Stn	% Pl
SCNC370a									0	95	0	5
SCNC370b	5.8	5.5	6.2	6.1	21	21	16	34	0	100	0	0
SCNC351a												
SCNC351b	6.8	6.8	6.4	6.8	49	39	47	36	0	95	0	5
SCNC348a									5	85	0	10
SCNC348b	6.6	6.4	6	6.3	7	24	15	32	0	70	0	30
SCNC346a	5.8	5.6	6.3	6.4	22	32	37	22	0	90	5	5
SCNC346b	6	5.6	5.9	6.4	32	30	23	25	0	90	5	5
SCNC342a	5.8	5.8	5.8	5.9	24	19	22	15	5	75	0	20
SCNC342b	6.2	6.4	6.3	6.4	15	25	19	5	5	75	0	20
SCNC334a	5.8	5.8	6	5.8	22	25	12	5	5	85	0	10
SCNC334b	5.7	5.8	6.3	5.6	20	35	25	30	5	85	0	10
SCNC329a	5.6	5.8	6.4	6	2	10	30	35	2	80	0	18
SCNC329b	5.5	5.4	5.8	5.7	58	60	64	49	0	95	0	5
SCNC321a	5.9	5.9	6.5	6.2	45	30	57	39	0	95	0	5
SCNC321b	6.9	6.8	6.9	6.9	30	26	45	59	0	95	0	5
SCNC319a	6	6.2	6.2	6.4	54	55	63	32	0	95	0	5
SCNC319b	6.7	6.6	6.6	6.7	38	45	55	18	0	95	0	5
SCNC313a												
SCNC313b	6.8	6.7	6.5	6.6	93	72	59	62	0	100	0	0
SCNC302a	5.9	5.9	6.2	5.6	18	19	22	22	5	85	0	10
SCNC302b	6	5.7	5.8	6.5	20	15	17	18	5	85	0	10
SCNC295a												
SCNC295b	5.9	5.8	6.8	6.3	3	4	11	12	10	40	0	50
SCNC291a												
SCNC291b	6.3	6.4	6.5	6.2	25	17	13	10	5	90	0	5
SCNC280a	6.2	6.7	6.4	6.1	55	85	60		2	93	0	5
SCNC280b	7	6.8	7	6.8	58	60	64	49	0	95	0	5
SCNC274a									0	100	0	0
SCNC274b	5.7	6	6.5	5.9	6	20	6	20	5	90	0	5
SCNC258a									0	95	0	5
SCNC258b	5.7	5.9	6	5.7	30	22	17	26	2	90	3	5
SCNC256a												
SCNC256b	7	7	6.8	6.9	45	48	29	48	0	98	0	2
SCNC241a									0	90	0	10
SCNC241b	6.8	6.8	6.7	6.8	9	30	14	26	0	95	0	5
SCNC238a	5.8	5.7	5.6	5.5	28	20	28	25	0	95	0	5
SCNC238b	6.2	6	6.8	6	15	44	18	23	0	95	0	5
SCNC234a									2	80	0	18
SCNC234b	6.2	6.3	6.7	6.3	18	6	20	10	2	80	0	18

Table 2.2 (page 4 of 4)

Sample Code	pH	pH	pH	pH	Lit 1	Lit 2	Lit3	Lit4	% Bare	% Lit	% Stn	% Pl
SCNC209a	5.6	5.6	6.1	6	14	20	29	18	0	13	2	5
SCNC209b	6.6	6.6	6.4	6.8	21	21	25	38	0	13	2	5
SCNC199a	5.9	6	6.2	6.2	5	13	3	2	10	10	0	80
SCNC199b	5.9	6	6.2	6.1	15	5	2	12	10	10	0	80
SCNC198a	5.8	6.3	6.2	6.2	12	24	28	38	0	70	0	30
SCNC198b	6.2	6	6.1	6.2	22	7	30	33	5	90	0	5
SCNC187a	5.8	5.8	6	6.2	25	35	20	25	0	90	0	10
SCNC187b	6.3	6.2	6.3	6	18	16	21	24	0	95	0	5
SCNC181a												
SCNC181b	5.8	6	6	6	30	27	27	25	5	85	0	10
SCNC161a												
SCNC161b	6.8	6.6	6.3	6.7	25	25	22	24	0	95	0	5
SCNC158a												
SCNC158b	6.5	6.2	6	6	30	27	27	25	0	98	0	2
SCNC150a	5.8	6	6.5	6.2	2	5	32	35	5	90	0	5
SCNC150b	6.8	6.2	5.6	7	48	10	48	25	5	95	0	0
SCNC136a	5.8	5.8	6	6.2	15	18	5	5	2	90	0	8
SCNC136b	6.5	6.2	6	5.9	22	16	18	18	2	90	0	8
SCNC123a	6.3	5.8	5.9	6	34	30	45	37	0	95	0	5
SCNC123b	6.7	6.3	6.5	6.7	26	38	32	33	0	95	0	5
SCNC96a	6.3	5.7	6.3	6.2	33	25	25	47	0	90	0	10
SCNC96b	6.2	6.2	5.8	5.8	32	35	36	28	0	90	0	10
SCNC82a	5.4	4.7	5.9	5.5	35	23	15	17	0	95	0	5
SCNC82b	6.4	6.2	5.8	6	28	20	15	23	0	95	0	5
SCNC59a												
SCNC59b	5.8	5.4	6.1	6	9	12	17	28	5	75	0	20
SCNC38a												
SCNC38b	6.4	6.8	6.8	6.7	30	33	47	25	0	98	0	2
SCNC19a												
SCNC19b	6.5	6.5	6.5	6.6	30	40	15	20	0	98	0	2
SCNC16a	6.7	6.6	6.8	6.8	34	34	34	25	0	98	0	2
SCNC16b	6.7	6.6	6.8	6.8	34	34	34	25	0	98	0	2

Table 2.3 (1 of 2 pages)

Sample Code	Site	*S. abdita*	*S. clypeata*	*S. creightoni*	*S. dietrichi*	*S. louisianae*	*S. laevinasis*	*S. membranifera*	*S. missouriensis*	*S. ohioensis*	*S. ornata*	*S. pilinasis*	*S. pulchella*	*S. pergandei*	*S. reflexa*	*S. rostrata*	*S. talpa*	0.20 ha subsample abundance	Species Richness
SCNC370a	370	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	3	2
SCNC370b	370	0	0	0	0	0	0	0	0	1	1	0	0	0	1	7	0	10	4
SCNC351a	351	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	1
SCNC351b	351	0	1	0	0	0	0	0	0	0	9	0	0	0	0	0	0	10	2
SCNC348a	348	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC348b	348	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC346a	346	0	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	5	2
SCNC346b	346	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	4	8	2
SCNC342a	342	0	0	0	0	0	0	0	0	1	9	0	0	0	0	1	1	12	4
SCNC342b	342	0	0	0	0	0	0	1	1	1	37	0	6	0	0	1	0	47	6
SCNC334a	334	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC334b	334	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC329a	329	0	0	0	0	0	0	0	0	6	3	0	0	0	1	0	0	10	3
SCNC329b	329	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC321a	321	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC321b	321	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	4	1
SCNC319a	319	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	3	2
SCNC319b	319	0	0	0	0	0	0	0	0	20	8	0	0	0	5	0	0	33	3
SCNC313a	313	0	2	0	0	0	0	0	0	6	0	0	0	0	0	0	0	8	2
SCNC313b	313	0	0	0	0	0	0	0	0	2	4	0	0	0	0	0	0	6	2
SCNC302a	302	0	0	0	0	0	0	0	0	3	1	0	0	0	1	2	0	7	4
SCNC302b	302	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	4	2
SCNC295a	295	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC295b	295	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC291a	291	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC291b	291	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
SCNC280a	280	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	4	2
SCNC280b	280	0	1	0	0	0	0	0	0	7	0	0	0	0	0	0	0	8	2
SCNC274a	274	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC274b	274	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1
SCNC258a	258	0	0	0	0	4	0	0	0	6	1	0	0	0	1	0	0	12	4
SCNC258b	258	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	1
SCNC256a	256	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC256b	256	0	1	0	0	0	0	0	0	2	1	0	0	0	0	2	0	6	4
SCNC241a	241	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC241b	241	1	3	0	0	15	0	0	0	11	9	0	0	0	0	0	0	39	5
SCNC238a	238	0	0	0	0	3	0	0	0	3	5	0	0	0	0	0	4	15	4
SCNC238b	238	0	0	0	0	0	0	0	0	3	10	0	0	0	0	2	0	15	3
SCNC234a	234	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
SCNC234b	234	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 2.3 (2 of 2 pages)

Sample Code	Site	*S. abdita*	*S. clypeata*	*S. creightoni*	*S. dietrichi*	*S. louisianae*	*S. laevinasis*	*S. membranifera*	*S. missouriensis*	*S. ohioensis*	*S. ornata*	*S. pilinasis*	*S. pulchella*	*S. pergandei*	*S. reflexa*	*S. rostrata*	*S. talpa*	0.20 ha subsample abundance	Species Richness
SCNC209a	209	0	0	0	0	1	0	0	0	3	4	0	0	0	0	0	0	8	3
SCNC209b	209	0	0	0	0	0	0	0	0	6	6	0	0	0	0	0	1	13	3
SCNC199a	199	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	6	1
SCNC199b	199	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC198a	198	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1
SCNC198b	198	0	0	0	0	0	0	0	0	0	0	0	3	0	0	10	0	13	2
SCNC187a	187	0	0	0	0	0	0	0	0	0	4	0	0	0	0	4	0	8	2
SCNC187b	187	0	0	0	0	6	1	0	0	1	10	0	0	0	1	7	0	26	6
SCNC181a	181	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC181b	181	0	0	0	0	1	0	0	0	1	0	0	4	0	0	0	0	6	3
SCNC161a	161	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	3	2
SCNC161b	161	0	5	0	0	0	0	0	0	4	5	0	4	0	0	7	0	25	5
SCNC158a	158	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	5	1
SCNC158b	158	0	0	0	0	0	0	0	0	2	2	0	0	0	0	16	0	20	3
SCNC150a	150	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	3	2
SCNC150b	150	0	0	0	0	2	0	0	0	0	7	0	0	0	1	1	0	11	4
SCNC136a	136	0	0	0	0		0	0	0	0	1	0	0	0	0	0	0	1	1
SCNC136b	136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SCNC123a	123	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
SCNC123b	123	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	5	8	4
SCNC96a	96	0	0	0	0	0	0	0	0	2	4	0	0	0	0	3	0	9	3
SCNC96b	96	0	4	0	0	4	0	0	0	17	1	1	0	0	1	19	0	47	7
SCNC82a	82	0	0	0	0	0	0	0	0	7	1	0	0	0	0	2	0	10	3
SCNC82b	82	1	0	0	0	1	0	0	0	28	0	0	0	0	0	31	0	61	4
SCNC59a	59	0	0	0	0	0	0	0	0	9	4	0	0	0	0	3	0	16	3
SCNC59b	59	1	0	0	0	0	0	0	0	5	2	0	0	1	0	6	0	15	5
SCNC38a	38	0	0	0	0	0	0	0	0	0	2	0	0	0	0	3	0	5	2
SCNC38b	38	0	0	0	0	0	0	0	0	0	3	0	0	0	0	23	0	26	2
SCNC19a	19	0	0	0	0	0	0	0	0	0	15	0	0	0	1	0	0	16	2
SCNC19b	19	0	0	0	0	0	0	0	0	19	4	0	0	0	0	4	0	27	3
SCNC16a	16	1	0	0	0	0	0	0	0	9	2	0	0	0	1	6	0	19	5
SCNC16b	16	0	0	0	0	8	0	0	0	2	0	0	0	0	0	13	0	23	3

Table 2.4 (1 of 2 pages)

Site	Latitude	Longitude	El.	Topography 1	Topography 2	Forest Type	Veg. size
SCNC370	33.98048	-83.38115	614	Bottomland	Field	MFF	Large
SCNC351	33.98233	-83.38282	639	Slope	Ridge	MPH	Medium
SCNC348	33.98117	-83.37987	613	Bottomland	Field	MFF	Large
SCNC346	33.98175	-83.38060	639	Flat Forest	Flat Forest	MHP	Large
SCNC342	33.98173	-83.38250	633	Slope	Slope	MHW	Large
SCNC334	33.98233	-83.38115	624	Bottomland	Slope	MHW	Large
SCNC329	33.98170	-83.38362	628	Slope	Bottomland	MHW	Large
SCNC321	33.98255	-83.38233	644	Ridge	Slope	MPH	Medium
SCNC319	33.98232	-83.38347	624	Bottomland	Slope	MHW	Large
SCNC313	33.98343	-83.38258	638	Slope	Ridge	MPH	Large
SCNC302	33.98322	-83.38330	617	Flat Forest	Bottomland	MHW	Large
SCNC295	33.98428	-83.38373	615	Bottomland	Bottomland	HWF	Medium
SCNC291	33.98450	-83.37948	613	Bottomland	Bottomland	MHW	Medium
SCNC280	33.98408	-83.38213	647	Ridge	Ridge	MPH	Large
SCNC274	33.98428	-83.38430	617	Bottomland	Bottomland	MHW	Large
SCNC258	33.98413	-83.38153	633	Slope	Bottomland	MHW	Large
SCNC256	33.98533	-83.38103	646	Slope	Ridge	MHW	Large
SCNC241	33.98562	-83.38208	627	Slope	Flat Forest	MHP	Medium
SCNC238	33.98370	-83.38348	611	Bottomland	Slope	MHW	Medium
SCNC234	33.98362	-83.38458	616	Bottomland	Bottomland	MHW	Large
SCNC209	33.98605	-83.38177	635	Ridge	Slope	MHW	Medium
SCNC199	33.98652	-83.37715	618	Field	Field	F	Small
SCNC198	33.98633	-83.37780	618	Bottomland	Field	MHW	Large
SCNC187	33.98652	-83.38405	618	Flat Forest	Flat Forest	MPH	Large
SCNC181	33.98707	-83.37853	618	Bottomland	Bottomland	MHW	Medium
SCNC161	33.98732	-83.38180	633	Flat Forest	Ridge	MHP	Medium
SCNC158	33.98728	-83.38443	619	Flat Forest	Flat Forest	MHW	Medium
SCNC150	33.98763	-83.37925	621	Slope	Bottomland	MHP	Large
SCNC136	33.98793	-83.38522	613	Bottomland	Bottomland	HWF	Large
SCNC123	33.98857	-83.38285	639	Flat Forest	Flat Forest	PF	Medium
SCNC96	33.98887	-83.37857	620	Flat Forest	Flat Forest	MPH	Large
SCNC82	33.98850	-83.38458	652	Flat Forest	Bottomland	MHW	Medium
SCNC59	33.98943	-83.38038	638	Flat Forest	Flat Forest	MHP	Medium
SCNC38	33.98952	-83.38352	631	Flat Forest	Flat Forest	MPH	Medium
SCNC19	33.99020	-83.38293	641	Flat Forest	Flat Forest	MPH	Medium
SCNC16	33.99022	-83.38445	633	Flat Forest	Flat Forest	MPH	Medium

Table 2.4 (2 of 2 pages)

Site	Veg. 1	Veg. 2	Veg. 3	Soil Description	Sl. Dir.	Sl. Min	Sl. Max
SCNC370	Beech	Pine	Field	Clay		1	3
SCNC351	Pine	Gum	Mixed	Clay/Sand	244	3.5	9
SCNC348	Oak	Mixed	Field	Sand/Clay		0	1.5
SCNC346	Oak	Mixed	Pine	Clay		0	4
SCNC342	Oak	Beech	Mixed	Clay	185	1	20
SCNC334	Oak	Mixed	Mixed	Clay	340	0	40
SCNC329	Oak	Beech	Mixed	Clay	276	1	22.5
SCNC321	Pine	Gum	Mixed	Clay	185	0	50
SCNC319	Gum	Poplar	Grass	Clay	258	5	60
SCNC313	Pine	Gum	Oak	Clay/Sand	320	6	12
SCNC302	Oak	Poplar	Mixed	Clay	271	5	15
SCNC295	Cottonwood	Mixed	Mixed	Clay		0	0.5
SCNC291	Cottonwood	Cottonwood	Cottonwood	Clay		0	0.5
SCNC280	Pine	Oak	Gum	Clay/Sand		1	7
SCNC274	Beech	Cottonwood	Mixed	Clay		0	4.5
SCNC258	Oak	Cottonwood	Mixed	Clay	148	0	21
SCNC256	Oak	Hickory	Mixed	Sand/Clay	334	5	10
SCNC241	Gum	Pine	Mixed	Clay	274	1.5	5.5
SCNC238	Gum	Oak	Mixed	Clay	303	2	4
SCNC234	Beech	Cottonwood	Mixed	Clay		0	4
SCNC209	Oak	Mixed	Mixed	Clay	145	3	20
SCNC199	Grass	Grass	Grass	Clay/Sand		0	1
SCNC198	Hickory	Sycamore	Oak	Clay/Sand		0	2
SCNC187	Pine	Mixed	Mixed	Clay/Sand		1	4
SCNC181	Cottonwood	Cottonwood	Birch	Clay		0	1
SCNC161	Mixed	Gum	Pine	Clay/Sand		0.5	3.5
SCNC158	Gum	Poplar	Cottonwood	Clay		0.5	2
SCNC150	Oak	Pine	Gum	Clay	80	2.5	70
SCNC136	Cottonwood	Cottonwood	Gum	Clay		0	2
SCNC123	Pine	Pine	Gum	Clay/Sand		0	3
SCNC96	Pine	Gum	Oak	Clay/Sand	166	1	8
SCNC82	Gum	Mixed	Mixed	Clay		0	2
SCNC59	Mixed	Pine	Elm	Clay/Sand		0	4
SCNC38	Pine	Gum	Mixed	Sand/Clay		1	3
SCNC19	Pine	Pine	Gum	Clay/Sand		1	3
SCNC16	Pine	Mixed	Mixed	Sand/Clay		1	3

Table 2.5

Sample Code	site description	nearest tree	(DBH)	(m)	Veg. 1
SCNC342 R-01	Edge of Stump	Beech	146.5	3	Privet/Herb
SCNC342 R-02	Bottomland	Oak	232	1	Privet
SCNC342 R-03	Slope	Cottonwood	19.5	1.2	Cottonwood
SCNC342 R-04	Base of Slope	Basswood	107	3.5	Privet
SCNC342 R-05	Litter pile edge of rd & Forest	Oak	96	1.8	Sapling
SCNC342 R-06	Litter pile edge of rd & Forest	Oak	237	2	None
SCNC342 R-07	MHW	Oak	68	0.2	None
SCNC342 R-08	Depression in slope	Birch	515	1.3	Privet
SCNC342 R-09	Flat Woods	Ironwood	41.5	0.7	Ferns
SCNC342 R-10	MHW	Oak	142.5	1.4	Privet
SCNC342 R-11	Slope Tree Base	Beech	146.5	3	Litter
SCNC342 R-12	Bottomland	Oak	232	0	Privet
SCNC342 R-13	Slope	Basswood	107	0	Grass
SCNC342 R-14	MHW Slope	Beech	214	0	Poison Ivy
SCNC342 R-15	Beech	Elm	75	2.5	Vine
SCNC342 R-16	Tree Base Edge of Road	Oak	237	2	Privet
SCNC342 R-17	Slope Edge if Road	Pine	190	0	Sapling
SCNC342 R-18	Flat depression	Gum	120.5	0	Privet
SCNC342 R-19	Flatwoods	Poplar	342	0	Privet
SCNC342 R-20	Pine Log	Birch	55.5	0.6	Privet

Table 2.5 (continued)

Sample Code	ave L	n sticks	vol L	SM Ave.	pH Ave.	Humus (mm)	Slope Direction	Slope	% Bare	% Litter	% Stone	% Plant
SCNC342 R-01	22	2	2.75	10	6.7	0	-	0	5	90	0	5
SCNC342 R-02	12	3	1.75	70	6.2	0	-	0	5	95	0	0
SCNC342 R-03	36	1	3.50	40	6.7	15	-	45	5	95	0	0
SCNC342 R-04	33	1	2.25	75	6.1	2	225	30	0	95	5	0
SCNC342 R-05	39	11	3.75	45	6.4	25	330	15	0	100	0	0
SCNC342 R-06	38	8	4.25	50	6.2	20	305	40	5	9	5	0
SCNC342 R-07	45	3	3.50	55	6.3	3	285	4	0	100	0	0
SCNC342 R-08	30	3	3.00	35	6.6	6	257	7	0	95	0	5
SCNC342 R-09	21	4	1.75	35	6.7	3	-	0	0	85	0	15
SCNC342 R-10	17	2	3.25	20	6.7	8	292	10	0	100	0	0
SCNC342 R-11	7	4	4.50	15	6.8		0	30	10	80	5	5
SCNC342 R-12	18	8	3.00	100	6.2	5	211	10	10	85	0	5
SCNC342 R-13	33	8	3.76	20	6.8	6	245	43	10	85	0	5
SCNC342 R-14	36	8	3.75	30	6.8	12	239	70	15	5	0	5
SCNC342 R-15	90	3	4.00	35	6.8	45	252	20	5	90	5	0
SCNC342 R-16	39	10	4.00	30	6.8	8	251	17	15	80	0	5
SCNC342 R-17	25	9	3.00	30	6.7	57	290	20	5	90	0	5
SCNC342 R-18	32	3	3.25	60	6.3	10	310	12	0	100	0	0
SCNC342 R-19	16	3	2.00	40	6.4	5	-	0	10	90	0	0
SCNC342 R-20	14	6	2.25	25	6.7	2	310	6	5	90	0	5

Table 2.6

Sample Code	*S. abdita*	*S. ohioensis*	*S. ornata*	*S. pulchella*	*S. reflexa*	*S. rostrata*	*Strumigenys* abundance	*Strumigenys* richness
SCNC342 R-01		17	1				18	2
SCNC342 R-02					2		0	0
SCNC342 R-03		3	4				7	2
SCNC342 R-04							0	0
SCNC342 R-05	1	6			1		8	3
SCNC342 R-06		2			2		2	2
SCNC342 R-07		1	1				2	2
SCNC342 R-08							0	0
SCNC342 R-09		6			1		7	2
SCNC342 R-10							0	0
SCNC342 R-11		72	3		2		77	3
SCNC342 R-12		2	2				4	2
SCNC342 R-13		15	4		3		22	3
SCNC342 R-14		4	1		3		7	3
SCNC342 R-15			7	7	2		16	3
SCNC342 R-16		9	2		2	6	19	4
SCNC342 R-17		11	1				12	2
SCNC342 R-18		1					1	1
SCNC342 R-19			1			5	6	2
SCNC342 R-20		3	2				5	2

2.10 Appendix I: Sample codes, descriptions of variables, and descriptions of field measurements

2.10.1 Field Equipment

Garmin® etrex Summit HC GPS, AMS 10.2 cm diameter soil core, 1 cm diameter mini soil core, 1cm grid litter sifter, Kelway® soil tester for pH, General® Dsmm500 moisture meter, Extrech® pocket IR201 infrared thermometer for litter and soil surface temperature, REI® mercury thermometer for ambient temperature, a string level and angle finder to measure slope grade, a magnetic compass for slope-face direction, a dbh tape for tree measurements, a metric ruler to measure litter and soil layer, 3.75 liter bags to measure sifted material, breathable Santos Winkler sacks for litter storage until ants extraction of either Berlese or Winkler extraction method, and a 25 m field tape to measure quadrats, other equipment listed below.

2.10.2 Site variables taken in 0.20ha sites and microsites

Sample Code. The unique number, letter, or combination associated with a particular sample within a site. The sample code will correlate to any specimens or data within a unique sample.

Site. The 0.20 ha site number, labeled from top left to bottom right of SCNC.

Local Habitat. 0.20 ha site within a region.

Extraction. The method used to extract litter dwelling arthropods from sifted leaf litter.

Microsite. $1m^2$ area within a local habitat including all woody debris and consisting of leaf litter, leaf mold, and humus layers.

Date. The day I took litter collections.

Temp A. The difference between the average temperature of air taken at four shaded points within a 0.20 ha site and the average daily temperature of Athens, GA on that day as reported by weatherunderground.com. Temperatures recorded in Celsius.

Temp L. The difference between the average temperature of the top of leaf litter taken at four shaded points within a 0.20 ha site and the average daily temperature of Athens, GA on that day as reported by weatherunderground.com. Temperatures recorded in Celsius.

Temp S. The difference between the average temperature of the layer of soil and the average daily temperature of Athens, GA on that day as reported by weatherunderground.com. I took temperature readings at four subsampled points where I had removed top layers of leaf litter and humus within a 0.20 ha site. Temperatures recorded in Celsius.

El. Elevation of the center of the site in meters.

GPS. The geographical coordinates recorded for each sample at the nearest possible point to the midpoint of the sample. I confirmed GPS coordinates taken in the field with google earth®.

Top 1 and Top 2. Top 1 refers to the dominant topography, Top 2 the secondary topography.

Site Topography Terminology for Top 1 and Top 2

1. Bottomland. (Flood Plain and Marsh) An area defined by seasonal flooding. Typically the lowest elevation forest type next to a river or flowing body of Water.
2. Flat Forest. A forest type with no or undefined slope and is elevated above the flood zone.
3. Ridge. A forest type at the peak of an elevated terrain with slopes on either side.
4. Slope. A forest type on sloped terrain.

Forest (generalized tree community)

1. MHW. Mixed Hardwood Forest
2. MPH. Mixed Pine and Hardwood forest. Pine is dominant.
3. MHP. Mixed Hardwood and Pine forest. Hardwood is dominant.
4. PF. Pine forest.
5. HWF. Hardwood forest (dominated by a single tree species)
6. FD. Field

Vegetation Size. Use the dominant vegetation type to determine size class.

1. Small < 80 dbh
2. Medium >80 & < 200 dbh
3. Large >200 dbh

Vegetation 1, 2 & 3. Place dominant vegetation in Vegetation 1, secondary vegetation in Vegetation 2, and tertiary vegetation in Vegetation 3. When no dominant existed I listed vegetation type as Mixed. When only one tree exists, it is listed multiple times.

SIMULTANEOUS READINGS - I took Soil Moisture, pH, and Leaf Litter readings in the same place, so that SM1, pH1, and Lit 1 correlate to the same exact location. I took four readings over an even transect bisecting the sample area.

SM1-SM4. Soil moisture readings 1 through 4.

SM Ave. Average soil moisture of all readings for the same site, from one or two sets of measurements.

pH1-pH4. pH readings 1 through 4

pH Ave. Average pH of all readings for the same site, from one or two sets of measurements.

Lit 1 - Lit 4. Leaf litter depth measurements in cm 1 through 4. Includes:

TopLit. Freshly fallen and not yet decomposing leaf layer.

Lmold. Leaf mold depth, depth of compacted decaying litter below

Hms. Humus depth, depth of organic layer between soil and leaf mold.

Lit Ave. Average litter depth (cm) of all readings for the same site, from one or two sets of measurements.

Soil Description. The type of soil. Defined as **Clay, Loam**, or **Sand**.

Sl. Dir. Slope direction. Take slope direction measurement in one-degree increments of 360 degrees. 360/0 degrees is North.

Sl Min. The minimum angle of slope at a sample site. The angle is measured in degree difference between level and the ground below.

Sl Max. The maximum angle of slope at a sample site. The angle is measured in degree difference between level and the ground below.

% Coverage. The area covered in each category. Estimated coverage data is collected in terms of presence or absence of each category within a 15 cm diameter circle with center point at every tenth meter along a 50 m transect. The transect, with 25m point centered in the 0.2 ha local habitat, will run along the diagonal SW to NE corner of the site. I then normalized this data percent of each category present. Microsite % coverage represented actual space each category represents.

%Bare. The amount of soil exposed in the sample area.

%Lit. The amount of litter covering the sample area.

%Stn. The amount of stone or rock exposed in the sample area.

%Pl. The amount of vegetative cover in the sample area.

2.10.3 Additional microsite measurements

Stk Ct. The number of sticks, and or fallen branches within a site

Stk Vol. The volume of woody debris (sticks and branches) calculated by summed length x diameter of all sticks or branches greater than 5 cm within microsite.

Stk Dia. The diameter of the largest branch or stick.

2.11 References

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3. Chapter 3. Biogeography of Nearctic *Strumigenys.*

3.1 ABSTRACT

Different species of a lineage often occur in biogeographic regions having different climates. This pattern can arise through different evolutionary paths. In some cases, changes in climatic tolerance can evolve quickly, and one or more lineages can adaptively radiate rapidly into different climatic niches. In other cases, species within clades many exhibit climatic niche conservatism, and their distribution among different climates in newly colonized biogeographic regions simply reflects the climatic conditions of their origination areas.

The species-rich and globally widespread genus *Strumigenys* is an excellent monophyletic taxon of ants in which to examine how dispersal and speciation influence biogeographic patterns in diversity and how these biogeographic patterns likely influence the species composition of *Strumigenys* communities. The Nearctic *Strumigenys* are a multi-lineage assemblage of 56 species that are known to occur across a broad range of climates. Here we produced a globally representative *Strumigenys* phylogeny using a RAD-sequence approach to infer phylogeographic histories and inform taxonomic relationships between species and their mandibular morphologies. We also test two hypotheses for the assembly of biogeographic patterns in Nearctic *Strumigenys*. 1) Adaptive Radiation: After lineage(s) got to the Nearctic, they adaptively radiated into new climatic regions different from those from where they originated. This hypothesis predicts that more closely related species (the same lineage) occupy more dissimilar climatic ranges than expected at random. 2) Evolutionary Conservatism: Multiple lineages from different clades colonize the region, but they maintain their ancestral climatic tolerances within each lineage and colonize mew regions having climates similar to those of their ancestral biogeographic regions. Thus, climatic niche diversity within

each region reflects deep evolutionary climatic niche conservatism, retaining adaptations to climates in the Nearctic most similar to their ancestral climates. In this case, we predict more closely related species (of the same lineage) will occupy more similar climatic ranges.

The molecular-based phylogeny confirms *Strumigenys* are monophyletic with ancestors of Old World origin. The phylogeny also reveals that major morphological characters used by *Strumigenys* taxonomists are poor indicators of phylogenetic relationships. Results of climate and phylogenetic comparisons match predictions of the Evolutionary Conservatism hypothesis. Radiations within *Strumigenys* have a strong biogeographic signal and the majority of *Strumigenys* occurring in the Nearctic evolved from a common ancestor of temperate northeast Asian origin. The remaining U.S. fauna either dispersed from the Neotropics, or arrived recently probably through human-assisted dispersal. Ranges of migrant or introduced species within the U.S. are consistent with average annual temperature and rainfall of ranges they occupy outside of the U.S.

3.2 INTRODUCTION

Dispersal and speciation are major influences on geographic patterns of diversity on large spatial scales (Ricklefs 2004, Dunn, Agosti et al. 2009, Economo, Sarnat et al. 2015). Among the questions that arise include: When species disperse to new geographic regions, to what extent are their new geographic ranges defined or constrained by the environments of their origins? Conversely, what ability do immigrant species have to adapt, evolve, and radiate into new environments not previously encountered? Answering these questions is important for understanding and interpreting phylogeographic patterns of diversity in general. To examine phylogenetic relationships of *Strumigenys* occurring in the U.S. we used a RAD-sequence approach. We included 43 of the 56 known *Strumigenys* species occurring in the Nearctic along

with 32 species to represent known global diversity. We used this phylogeny to describe phylogeographic patterns and infer the evolutionary histories of Nearctic *Strumigenys*. We obtained locality records from twelve museum collections and available databases to describe the geographic and climatic ranges of native and non-native species. We then tested the hypothesis that the climates where non-native species originated predict the contemporary climatic ranges of these species in the United States after introduction. If species of the same lineage occupy similar environments (phylogenetic niche conservation), this would support Evolutionary Conservatism of Nearctic *Strumigenys*. Alternatively, if species of the same lineage occupy more dissimilar environments, this would support Adaptive Radiation of Nearctic *Strumigenys*. We compare these occurrences and co-occurrences of climatic and geographic ranges of species across the U.S. in large 60,000 km^2 bioregions.

To determine the appropriate bioregion scale to compare *Strumigenys* assembly across the U.S., there needed to be enough bioregions that were large enough to capture gross changes in climates across the U.S., and contain areas of similarly large collection efforts. I obtained collection records from musuems and supplemented those with collections reported in publications. I chose the bioregion scale of 60,000 km^2 as this scale best represented collection efforts and a sufficient number of bioregions to statistically compare. Bioregion climates differed from each other and represented all climates where *Strumigenys* occur (see methods for data collection). I used these bioregions to produce distance decay curves of *Strumigenys* assembly similarity across geographic distance. I used these distance decay curves and bioregions to describe range overlap of U.S. species as well as to test assembly hypotheses. For example, if *Strumigenys* assemblies of a lineage are dissimilar over small geographic distances, the distance-

decay curve will have a strong negative slope. If changes in geographic distance co-vary with changing climates and lineage dissimilarity, species within a lineage are ecologically dissimilar.

To assess environments of bioregions, we chose two climate variables. Mean Annual Temperature (MAT) and Precipitation in Driest Quarter (PDQ). MAT and annual precipitation are major predictors of vegetative formations and ant diversity and describe the environmental ranges correlating habitats with ant species (Holdridge 1947, Dunn, Agosti et al. 2009, Economo, Klimov et al. 2015). For this study, we chose to use MAT and PDQ. Researchers typically use MAT but not PDQ to describe environmental ranges of species. We chose PDQ instead of annual precipitation for several reasons. The first reason is that PDQ co-varied less with MAT than annual precipitation. The second reason is that *Strumigenys* are Collembola specialists and Collembola require moisture to reproduce and are most abundant in moist environments. Assuming *Strumigenys* are limited by prey abundance, they will be less abundant in areas prone to extended dry periods. PDQ is a better estimator of the lower moisture limits that species can tolerate in terms of both prey abundance and death due to desiccation (Petersen and Luxton 1982, Hopkin 1997).

The United States *Strumigenys* fauna is composed of native and non-native species with most non-native species having been described as recently arriving exotics of mostly tropical and subtropical native ranges, although one non-native, *S. hexamera* has a more temperate non-U.S. distribution (Wetterer 2011, Joe A. MacGown1 2012, MacGown 2012, Wetterer 2012, Wetterer 2012, Moreau and Bell 2013, Wetterer 2013, Deyrup 2016). Two other species *S. boneti* and *S. louisianae* are of likely Neotropical origin and have continuous ranges from the Neotropics into North America and probably migrated to the U.S. on their own (Deyrup and Cover 2009). By assuming the contemporary climate ranges a majority of species within a lineage occupy

indicated ancestral conditions, we deduced the biogeographic origin of species. Using the RAD-seq generated phylogeny and by assessing contemporary environments they occupy, we attempt to reconstruct the original environments in which species evolved.

Strumigenys belong to the subfamily Myrmicinae and to the tribe Attini. Their most closely related genera are *Pilotrochus* of Madagascar and the Neotropical genus *Phalacromyrmex* (Ward, Brady et al. 2015). Other notable ant genera in the Attini tribe are *Acanthognathus, Atta, Cephalotes, Colobostruma, Daceton, Eurhopalothrix, Microdaceton,* and *Pheidole.* The latter four genera include ants with specialized trap-jaw mandibles common to many *Strumigenys* species and were all previously placed in the tribe Dacetini (Bolton 2000a, Bolton 2000b). *Strumigenys* taxonomic placement as well as internal taxonomic relationships have remained unresolved by morphological taxonomic treatments, although recent phylogenetic evidence suggests *Strumigenys* is monophyletic. (Bolton 2000a, Bolton 2000b, Baroni Urbani and de Andrade 2007). The morphological treatments of *Strumigenys* were confused in part due specialized trap-jaw mandibles now known to be of at least three independent originations within the genus (Ward, Brady et al. 2015).

Two-thirds of *Strumigenys* species have derived and specialized power-amplified mandibles (PAM) commonly called “trap-jaw” ants, and about one-third of *Strumigenys* have ancestral mandibles (non-PAM and typical to most ants) that open and close through muscle contractions alone. “Trap-jaw” is named after the mechanical spring-loaded “trap-jaw” snares commonly used by fur trappers. In PAM *Strumigenys* the labrum, which in typical ants functions to close and protect the more delicate maxilla-labial mouthparts, has been modified to function as a mandibular catch-and-trigger mechanism. The labrum in PAM species consists of a modified lateral cornulae with a concave indentation to house a tooth-like process (termed a basal

mandibular process) in a latch-in-pocket manner. While mandibles are open and in latched position, muscles contract and load biological springs (thin flexible cuticular tissues termed apodemes that attach closing muscles to mandibles). The labrum closing muscle pulls the labrum down, disengaging the mandible process from the labrum and allows mandibles to swing shut through stored elastic energy, thereby amplifying the power of mandible closure. Mechanoreceptor chemo-sensors that look like elongate hairs extend anteriorly to the head from the labrum. When stimulated, they trigger labrum-closing muscles to contract and release the latched mandibles. It is not the movement of the labrum that differs between non-PAM mandibles and PAM *Strumigenys*, but the jaws operated by the trigger mechanism. In each of three known repeated originations of trap jaws in *Strumigenys*, the morphological changes of the mandible and the labrum were essentially identical, which led to the taxonomic confusion in this genus.

Strumigenys occurring in the United States are of both PAM and non-PAM morphotypes. All PAM species occurring in the U.S. also occur in other biogeographic regions (Neotropics, Australasia, and Afrotropics) and probably either dispersed by non-anthropogenic means to the U.S. or immigrated through human-assisted dispersal. The large majority of North American *Strumigenys* are native non-PAM species (Deyrup, Davis et al. 2000, Deyrup and Cover 2009, Deyrup 2016). These species were previously placed in *Smithistruma* (Brown 1948) and *Pyramica* (Bolton 1999) prior their current placement in *Strumigenys* (Smith 1860c) (Baroni Urbani and de Andrade 2007). Recently acquired sequence data have placed at least two species of the native North American *Strumigenys* fauna (*S. chiricahua,* and *S. pulchella*) into lineages originating in Asia or Papua New Guinea (Moreau and Bell 2013, Ward, Brady et al. 2015). Deyrup and Cover (Deyrup and Cover 2009) also hypothesized the North American non-PAM

native species to be of east Asiatic origin and arriving in North America following the spread of warm-temperate deciduous forests of the Arcto-Tertiary Geoflora period. However, this warmer period began in the late Mesozoic and a cooling trend started in the mid-Cenozoic period about 30 million years ago. This timetable is problematic because the genus *Strumigenys* is probably not more than 35 million years old and native non-PAM Nearctic species are estimated to have split from nearest Asiatic or Papua New Guinean ancestors between 7-10 mya (Moreau and Bell 2013, Ward, Brady et al. 2015). Even so, Dominican amber specimens between 25 and 12 mya also exhibit morphological traits similar to the native North American non-PAM species. Age estimates of Dominican amber support the hypothesis that these *Strumigenys* could have been present in North America at the end of the Arcto-Tertiary Geoflora period. However, as we indicated above, placement of species in this genus on the basis solely of morphology has not proven to be reliable. Native non-PAM Nearctic species have very similar morphologies to species of several biogeographic realms including Madagascar, Indonesia, Oceania, and the Neotropics. Moreover, species of the Afrotropics and Dominican amber are just as likely to be of Neotropical origin as of Asiatic. Just as PAM species evolved convergent morphologies in different biogeographic regions, morphological similarities in non-PAM species are likely to be convergent as well. By means of a dated and a molecular phylogeny that better represents both the morphological and biogeographic diversity of the genus, we aim here to untangle the morphological and phylogenetic relationships of North American *Strumigenys* while concurrently testing biogeographic assembly hypotheses to explain the relationships between phylogeny and morphology to geography and climate.

3.3 METHODS

3.3.1 DNA Sequencing and Phylogenetic Inference

We based our phylogenetic analysis on markers generated from Restriction site Associated DNA Sequencing (RAD-seq) (Baird, Etter et al. 2008), using protocols specifically designed for degraded samples. This allowed us to use a broad range of material including older museum samples in order to maximize coverage across *Strumigenys* species. We first used a non-destructive DNA extraction method following Tin et al. (Tin, Economo et al. 2014) by soaking it overnight in a chaotropic buffer. The DNA was then bound to magnetic beads and washed prior to library preparation. We prepared RAD-tag libraries following Tin et al. (Tin, Rheindt et al. 2015) using a Biomek® FXP Laboratory Automation Workstation (Beckman Coulter) to perform all of the liquid handling steps up to PCR. We performed sequencing on an Illumina Hi-Seq. We designed the barcodes following Bystrykh (Bolger, Lohse et al. 2014). We used Trimmomatic (Bolger et al. 2014) to filter by quality and trim the sequences to 41bp (parameters SLIDINGWINDOW:8:10 MINLEN:41 CROP:41).

We used ipyrad v.0.3.29 (Eaton 2014) for *de novo* sequence assembly using the default parameters. The assembly step aligns raw sequencing reads into homologous RAD loci (42 bp sequences) both within and among specimens, which can be then used for phylogenetic analyses. Consistent with many RAD datasets, there are a large number of loci but also a large number of missing data for most loci. Although these loci could be filtered out, previous studies have indicated that including large numbers of low-coverage loci is advantageous for phylogenetic inference due to hierarchical redundancy (Eaton, Spriggs et al. 2017), and this is consistent with what was found in our tests, thus we included all loci that were present in more than four

individuals. This left a matrix with 380,556 loci and 13,444,286 bp across 143 specimens, with 92% missing data.

To infer a maximum likelihood (ML) topology, we used ExaML v3.0.17 (Kozlov, Aberer et al. 2015), using the PSR (per site rate category) model with a GTR substitution matrix. We performed 100 bootstrap replicates to assess node support. To date the ML topology in relative time, we used reltime implemented in the software MEGA-CC v7 (Kumar, Stecher et al. 2016). For this analysis, we used a reduced matrix of higher coverage loci (65% matrix fill, ~20K bp), and the GTR substitution and local clock model. After dating the tree in relative time, we used the crown age (age of most recent common ancestor, 33mya) of *Strumigenys* inferred by the subfamily-wide analysis of Ward et al. (Ward, Brady et al. 2015) to set the absolute timescale of our phylogeny.

3.3.2 Obtaining Specimen Records to Estimate Geographic and Climatic Ranges of *Strumigenys*.

From September 2012 through July of 2017, I examined specimens from museums or visited museums with major *Strumigenys* holdings. I digitized locality records from collection labels associated with specimens and confirmed identifications of 14,922 specimens representing twelve entomological collections. Collections included Archbold Biological Station Entomology Collections (ABS, 5086 specimens), Clemson University Arthropod Collection (CUAC, 1 specimen), my personal collection (DBBC, 3232 specimens), Harvard University Museum of Comparative Zoology Entomology Collections (MCZ, 3 specimens), Los Angeles County Museum of Natural History (LACM, 1446 specimens), Louisiana State Arthropod Museum (LSAM, 153 specimens), Mississippi Entomological Museum at Mississippi State University (MEM, 3889 specimens), Sam Houston State University Entomology Collection (SHSUE, 188

specimens), Texas A&M University insect Collection (TAMUIC, 132 specimens), United States National Museum (USNM, 6 specimens), University of Georgia Collection of Arthropods (UGCA, 772 specimens), and The University of Central Florida Collection of Arthropods (UCFC, 14 specimens). Collection managers at ABS, MEM, and MCZ also confirmed identifications of specimens housed in their collections. Additional databases provided 14,641 locality records of *Strumigenys* species. I obtained 193 specimen locality records from Antweb.org, 444 from the MCZ (http://mczbase.mcz.harvard.edu/SpecimenSearch.cfm), and 5765 records from published papers available at antmaps.org and provided to me by developer Benoit Guenard. James Wetterer also provided an additional 8239 U.S. and global records for the following exotic species: *S. emmae, S. epinotalis, S. eggersi, S. gundlachi, S. hexamera, S. louisianae, S. lanuginosa, S. membranifera, S. margaritae, S. rogeri,* and *S. silvestrii*. To account for biases associated with records of multiple specimens from the same colony or population, repeated sampling at the same location, or duplications of localities referring to the same specimen located in museums as reported in publications, I rounded locality records GPS locations to five decimal places (accuracy < 2 m) and removed duplicate records for each species. I used this list of non-duplicated (unique) collections to estimate species abundances and ranges of species. I constructed estimated range maps using JMP® statistical software and Qgis® (JMP® 1989-20016, QGIS 2014, R-Core-Team 2017).

3.3.3 Choosing Bioregional Scale and Describing Geographic Range Overlap of Nearctic *Strumigenys*

To examine the relationship between geographic distance and dissimilarity of species, I mapped out 28 non-overlapping 60,000 km^2 areas in Qgis® (**Figure 3.18**). This spatial scale is appropriate to capture large-scale environmental variation across the United States. I chose these

specific non-overlapping bioregions to maximize numbers of *Strumigenys* records. Collection efforts tend to reflect areas in close proximity to collector locations, and they are also concentrated where collectors have attempted to complete faunistic surveys of ants. I adjusted for this collection bias by segregating sites having large collecting efforts, as revealed by collections data and published faunal surveys of ants, in separate bioregions. However, some bioregions with low numbers of species are not due to small collection efforts, but due to the relative rarity of *Strumigenys* in those bioregions.

For the following statistical analyses I wrote a custom script in *R* (R-Core-Team 2017). I discarded areas with fewer than 20 specimen locality records. The lower limit of 20 specimens assumes that the areas with low numbers of collections are not due to collection efforts, but due to the relative rarity of *Strumigenys* in those regions. For example, New Mexico is one of the most intensely surveyed U.S. state which has revealed more ant species than any other U.S. state (antweb.org) yet *Strumigenys* are relatively rare (three native species, but having more than 20 specimen locality records). Similarly, many states have no *Strumigenys* collections, yet have been intensively surveyed for ants (Wheeler 1917, Creighton 1950, Gregg 1963, Wheeler and Wheeler 1986, Talbot 2012). These regions represent bioregions where *Strumigenys* are actually rare or absent. I used sets of 20 randomly sampled (with replacement) specimen locality records from each area and repeated this sampling for each iteration for each 60,000 square km area. Random draws of 20 specimens with replacement provided distributions of species in each area to calculate Jaccard's dissimilarity index (1-Jaccard's index) for each pair of areas assuming collection records estimated true abundances. I replicated Jaccard dissimilarity between each pair of areas for each iteration and ran the model for 1000 iterations. To calculate the geographic distance of each grid in each replicate, I took the mean geographic location of the sampled

specimen locality records within that area and calculated distances between paired area means. I then plotted all paired geographic distances by the dissimilarity of species. I ran models using a minimum of 5 – 100 collection records and using between 100 and 1000 iterations for each model. Under 20 collection records I had large differences between 100 and 1000 iterations telling me there was high variance associated with a limited draw of community members to calculate Jaccard's index from. Excluding areas above 20 collection records resulted in a disproportionate number of bioregional areas on the peripheral range (where *Strumigenys* are known to be rare) being excluded resulting in no significant change of community similarity over distances within the central ranges of most species where *Strumigenys* are most abundant. I report on the 1000 iteration model using minimum collection records of 20 and 100 as the lower limit cutoff for bioregion inclusion.

I tested whether choice of areas produced a distance decay plot that differed from a distance decay plot generated by all possible areas using a moving window sampling design. Differing results could suggest bias in chosen demarcations of bioregions. I recovered no statistical difference in distance decay curves between chosen areas and the moving window sampling, and because of the increased time effort necessary for the computation of a moving window sampling design, I used chosen areas methods to examine climate influences on biodiversity patterns of U.S. *Strumigenys*.

3.3.4 Assessing Climatic and Geographic Ranges of Nearctic *Strumigenys*

I obtained two measures of climate, mean annual temperature (MAT) and precipitation of driest quarter (PDQ) from WorldClim.org version 2.0 (Fick and Hijmans 2017) for each unique species collection location using the *R* statistical package dismo (R-Core-Team 2017). One-way ANOVAs and each pair t-tests in JMP® tested for differences in climates (MAT and PDQ)

between species or species lineages. I tested for climatic differences in two ways, using climate records generated from only U.S. collected specimen locations, and using worldwide climate records of species that occur in the U.S. and elsewhere. If no differences exist between colonized climatic ranges between lineages, then more closely related species of lineages were able to diversify into more dissimilar environments than expected. This result would suggest Nearctic *Strumigenys* are phylogenetically niche differentiated and support the Adaptive Radiation hypothesis. However, lineages may occupy more dissimilar climatic ranges to each other and species within lineages may occupy more similar climatic ranges in colonized regions to those of their native regions. If true, closely related species did not diversify into more dissimilar environments than expected. This result would support phylogenetic niche conservation and therefore Evolutionary Conservatism. To estimate ranges and range overlap between species, I constructed polygon areas by connecting peripheral collection locations of each species using Qgis software. To infer biogeographic and climatic histories of *Strumigenys*, I categorized species in our phylogeny according to three climatic zones (temperate, subtropical, or tropical) according to the majority climatic zone their native ranges encompassed.

3.4 RESULTS

Our 74 taxon set phylogeny gave results broadly consistent with prior but more limited studies, showing monophyly of *Strumigenys* and support for an Old World origin, indicating either *S. ambatrix* (Madagascar) or *S. DBB003* (Australia) as basal to the rest of *Strumigenys* ((Ward, Brady et al. 2015)). In agreement with recent phylogenetic species placements (Ward, Brady et al. 2015), our phylogeny shows high degrees of geographic structure and is comprised of a basal Old World clade as one of five major monophyletic lineages, each associated with a biogeographic region. The five major biogeographic lineages are the basal clade in Old World

(Madagascar and Australasia), and the Neotropical (Central and South America), the Afrotropical (Africa, Europe, and Madagascar), the Australasian (India, Asia, and Australia), and the Nearctic (North America north of Mexico) clades **(Figure 3.1**).

The phylogeny reveals that *Strumigenys* present in the United States consist of a large Nearctic lineage of recently evolved species having a northeastern Asian ancestor similar to *S. canina*, a single undescribed species of a Neotropical lineage (*S. DBB079*), three species of Australasian origin (*S. membranifera* and *S. hexamera*) and eight species belonging to the Neotropical lineage. Previous phylogenetic work provides evidence of the origin of two additional species not included in our phylogeny due to inadequate loci retrieval, *S. emmae* originating within the Australasian lineage and *S. rogeri* originating within the Afrotropical lineage (Ward, Brady et al. 2015). Geographic collection records and supporting morphological characters placed the remainder of species collected in North America into biogeographic lineages (**Figure 3.1**) (Bolton 2000a, Bolton 2000b, Baroni Urbani and de Andrade 2007).

Dating the tree to crown estimates (Ward, Brady et al. 2015) provided time estimates of diversification and spread of *Strumigenys*. The *Strumigenys* dispersed to the Neotropics giving rise to a monophyletic clade arising at least 31 mya and consisting of basal non-PAM clades and a large derived PAM clade arising 25 mya. Though *Strumigenys* occurred in the Old World as long ago as 32 mya, the major lineage of African species started to diversify around 27 mya with PAM species arising from non-PAM African ancestors 22.5 mya. The Australasian lineage arose from non-PAM Afrotropical ancestors around 22.7 mya with PAM species arising from Australasian ancestors 16.5 mya. The Nearctic lineage of *Strumigenys* species is the youngest lineage of species (between 6 and 12 mya) and diversified quickly. This lineage contains 39 species (2 undescribed), with the deepest Nearctic node estimated to be 6.25 mya, averaging 6.24

species per million years for extant species (**Figure 3.1**). Our phylogeny shows clear support of PAM species evolving from non-PAM ancestors in three major biogeographic lineages. Although our phylogeny supports an Old world origin of *Strumigenys*, PAM species arose first in the Neotropical lineage, second in the Afrotropical, and most recently in the Australasian lineage.

We obtained 9646 unique locality collections for species collected in the U.S., 6142 U.S. records and an additional 3504 global locality records for species occurring in regions other than the U.S. Collection records provided estimated native and non-native ranges of species (**Figure 3.2, Figures 3.3-15**). Two species had contiguous ranges between the Central America and the U.S., *S. boneti* a species with a locally restricted range from Honduras to Brownsville, TX and *S. louisianae* a species with a large contiguous range from the temperate South America through Central America and the Caribbean into the United States. The remainder of species inhabiting the U.S. are of Neotropical origin. These species have disjunct ranges that suggest human-assisted introductions. These species include *S. eggersi, S. epinotalis, S. gundlachi, S. lanuginosa, S. margaritae* and *S. silvestrii*.

Species of the Nearctic lineage have overlapping ranges in the southeastern U.S. (**Figure 3.16**). Ranges of the Nearctic lineage of species are smaller or larger than expected at random (**Figure 3.17**). The seven species with ranges that do not extend east of the Mississippi River are either known from single collections, or have extremely narrow ranges, with *S. arizonica* having the largest estimated range of western species (360,846 km^2). Species occurring east of the Mississippi river have typically larger ranges. A majority of species ranges are greater than one million km^2, and a mean range size of about one tenth of the area of the United States (8.6 million km^2 ± SD 7.8 million km^2). There are twenty-eight non-overlapping 60,000 km^2

bioregions in the U.S. with at least 20 unique collections of *Strumigenys*. Species east of the Mississippi River occupy 9.4 ± SD 8.3 of these bioregions on average. Large overlapping ranges of species occurring in the U.S. produced a distance decay curve in which even bioregions that are the farthest apart still usually share at least some species (**Figure 3.19**). However, the species shared among bioregions separated by more than 2000 km are likely due to human-assisted dispersal because they all have been documented as recent arrivals in globally disparate continents (Wetterer 2011, MacGown, Wetterer et al. 2012, Wetterer 2012, Wetterer 2013). The Nearctic lineage have either eastern or western ranges and the most distant bioregions share no species within this lineage (**Figure 3.20).** The decrease in community similarity over distance disappears when using the twelve bioregions having at least 100 non-duplicated collection records of species belonging to the Nearctic lineage (**Figure 3.21**). All bioregions with more than 100 collection records all fall within the southeastern U.S. north of central Florida and east of the Mississippi River.

Of the *Strumigenys* species included in our phylogeny, 14% of *Strumigenys* occurring in the U.S. occurred outside the U.S. in sub-tropical or tropical locations and 93% occurring outside the U.S. have tropical to subtropical ranges. Ninety-seven percent of species in our phylogeny with temperate ranges belong to the Nearctic lineage or to a lineage containing their most closely related temperate northeastern Asian species (**Figure 21**). Of the five species most closely related to the Nearctic lineage, only one, *S. kempfi* has a tropical range. U.S. *Strumigenys* species originating outside the Nearctic occupy geographic regions with climatic ranges (precipitation in driest quarter, and mean annual temperature) in the U.S. consistent with climate ranges they occupy outside the U.S. (**Figures 3.23, Figures 3.24-25)**. These results are consistent with phylogenetic niche conservation and support the Evolutionary Conservatism hypothesis.

Global mean annual temperature records obtained from collection localities outside the U.S. show the ranges of mean annual temperatures that species occupy differ according to the biogeographic lineage to which they belong (ANOVA**,** R^2 = 0.45, Observations = 9606, F = 1982.5, p = < 0.0001, **Figure 3.26)**. Within the U.S. species occupy similar MAT climatic ranges that they occupy outside the U.S. and differ according to lineage (**Figures 3.26-27, Table 3.1**, **Figure 3.15**). Likewise, species occupy similar PDQ climatic ranges in the U.S. to those they occupy outside the U.S. and differ according to lineage (ANOVA**,** R^2 = 0.09, Observations = 6142, F = 147.72, **Figure 3.28-29.; Table 3.2, Figure 3.15**). Species of the native Nearctic lineage occupy cooler, more moist northern geographic ranges (**Figures 3.15-16, 3.26-29, Tables 3.2-3**). Collection records show species of the Nearctic lineage also occur in cooler and more moist locations within bioregions compared to species of tropical biogeographic lineages (**Table 3.3**). Again, these results are consistent with phylogenetic niche conservation and support the Evolutionary Conservatism hypothesis.

DISCUSSION

Strumigenys occurring in the U.S. either evolved in temperate Nearctic environments or arrived in the U.S. from warmer subtropical or tropical environments. The current pattern of biogeographic diversity of U.S. *Strumigenys* is consistent with the Evolutionary Conservatism hypothesis. More closely related species of the Nearctic lineage occupied cooler MAT and PDQ geographic areas and species of tropical and subtropical lineages occupied geographical ranges with similar MAT and PDQ climates they inhabit in their native ranges (**Figures 3.15 & 3.16**) Having PAM or non-PAM morphology shows no relationship to the climatic ranges of species. For example, PAM tropical species *S. emmae,* native to drier habitats (PDQ) and warmer

environments (MAT) of Australia, inhabits the driest and warmest environments in the U.S. of all *Strumigenys* species. Non-PAM species *S. hexamera* of more moist temperate environments had a more northern and cooler geographic range, similar to their presumed ancestral ranges, when compared to tropical species that tended to occupy warmer and southern U.S. ranges (*S. gundlachi, S. eggersi,* and *S. lanuginosa*).

During both glacial and inter-glacial periods, the temperate zone of the U.S. has always been disproportionately larger than sub-tropical and tropical zones. The Nearctic bioregion has only been as warm as now about 15% of the last 740 thousand years and current subtropical areas of the U.S. are much larger currently than in glacial periods. The number of ant species in the northern hemisphere is smaller than the number of ant species in the southern hemisphere and the most parsimonious explanation for this difference is that, in the northern hemisphere, there has been greater climate change since the Eocene which has led to higher extinction rates (Augustin, Barbante et al. 2004, Dunn, Agosti et al. 2009). Since larger areas typically support more species and larger populations of species, one would expect that more temperate-adapted species would persist in the U.S. through glacial inter-glacial periods compared to tropical- and subtropical-adapted species. This argument assumes that evolutionary adaptation to changing temperatures can only happened more slowly than environmental changes in temperature. It also assumes that dispersal is possible into new geographic ranges with similar environments. However, the effects of glacial/interglacial environmental flux on dispersal and speciation are not known. These climate fluctuations certainly promoted geographic range shifts, but how much speciation they caused is not clear, given that only about six new *Strumigenys* appeared in the Nearctic clade in the last million years, according to our time-referenced phylogeny. Perhaps

these climatic fluctuations have caused greater local extinction in U.S. populations of tropical or subtropical adapted species, which might explain the low numbers of these species.

We also uncover circumstantial evidence that species are able to quickly expand geographic ranges as migrant or introduced species show quick range expansion. The earliest U.S. records of *Strumigenys emmae* is 1945, for *S. membranifera* is 1943, and for *S. silvestrii* is 1953, and though multiple introductions are likely and introductions are likely prior to the earliest collection records, species have quickly expanded geographic ranges into similar environmental ranges they inhabit in native ranges. Their range expansions over the past ~70 years have occurred during recent history in a climate warming at rates greater than their recent evolutionary past (range sizes *S. membranifera* 667,000 km^2, *S. emmae* 61,000 km^2, and *S. silvestrii* 449,000 km^2). Assuming dispersal rate is at least as fast as *S. silvestrii* among other *Strumigenys* species, dispersal rates exceeded the dispersal rates needed to stay within currently occupied environmental ranges as the earth's climate has changed over glacial and interglacial periods (*S. silvestrii* would occupy the entire U.S. within 11,300 years at current estimated range expansion rate of 871 km^2 per year).

Whether or not dynamic glacial/inter-glacial promoted range expansion, contraction, and mixing of species, distance decay curves predict most native Nearctic lineage species are broadly ecologically tolerant and are not finely phylogenetically niche differentiated by MAT or PDQ environmental differences. Only one other species outside the Nearctic lineage is endemic to temperate US, *S.* DBB079, a species of a lineage with all other members being Neotropical in origin with most collections restricted to high altitude cooler environments. Bioregions having more than 100 collection records all fell within a centralized climatic and geographic range and had revealed no correlation between species similarities between U.S. bioregions and the

geographic distance between them. Further studies of *Strumigenys* diversity patterns and co-occurrences at finer geographic and environmental scales are needed to understand what processes of community assembly promote biogeographic diversity patterns.

CONCLUSION

The *Strumigenys* species included in our phylogeny indicates biogeography has strong phylogenetic structure in *Strumigenys*. The biogeographic ranges of species they contain support define lineages and support Evolutionary Conservatism in Nearctic *Strumigenys*. We show *Strumigenys* are Old World in origin and Neotropical *Strumigenys* are monophyletic arising from an Old World ancestor. The Nearctic lineage is a quickly radiating clade and the youngest clade of *Strumigenys*, arising between six and twelve mya. It is still not clear whether Asiatic ancestors of the Nearctic lineage of species could have migrated early enough to become trapped by 12 mya Dominican amber, but our dated tree predicts this is not likely. It is more probable that species found in the Dominican amber belong to an older non-PAM Neotropical lineage of species. Our phylogeny suggests non-PAM Neotropical species arrived from Old World ancestors more than 30 mya.

3.7 List of Figures

Figure 3.8. Global records of *Strumigenys hexamera. Strumigenys hexamera* is a tramp species of northeast Asian origin introduced into the southeastern United States.

Figure 3.9. Global records of *Strumigenys lanuginosa. Strumigenys lanuginosa* is a Central American species with an introduced range in southern Florida, United States.

Figure 3.10. Global records of *Strumigenys louisianae. Strumigenys louisianae* is a widespread Neotropical species that presumably migrated into the Nearctic region without human mediation.

Figure 3.11. Global records of *Strumigenys margaritae. Strumigenys margaritae* is a Neotropical species with an introduced range in the southeastern United States.

Figure 3.12. Global records of *Strumigenys membranifera. Strumigenys membranifera* is a tramp species of Asian origin.

Figure 3.13. Global records of *Strumigenys rogeri. Strumigenys rogeri* is a tramp species of African origin.

Figure 3.14. Global records of *Strumigenys silvestrii. Strumigenys silvestrii* is a tramp species from Neotropical origins.

Figure 3.15. Overlaid ranges of all species occurring in the United States. The phylogenetic distance level of all U.S. species. Overlaid ranges of species of Nearctic (Blue), Neotropical (red), Australasian (yellow), and Afrotropical (green) species that migrated or were introduced here. The average phylogenetic relatedness among all species is 0.013 (0.001 min, 0.025 max). Geographical data are consistent with the hypothesis that more closely related species of a lineage occupy similar environments to ones they evolved.

Figure 3.16. Overlaid ranges of *Strumigenys* belonging to the Nearctic lineage (clade). The phylogenetic distance level of only the Nearctic lineage of species. Ranges of species belonging to the Nearctic primarily occupy the southeastern United States tend to overlap with no abrupt demarcation between adjunct, non-overlapping ranges.

Figure 3.17. Distribution of range sizes for species belonging to the Nearctic lineage. Distribution of range sizes are skewed towards large and small range sizes and do not fit expectation of random Poisson distribution (red line). Actual distribution mean = 15.18, Lower CI 95% = 11.9, upper CI 95% = 18.5. Expected Poisson distribution mean = 15.18 lower CI 95% = 13.6, upper CI 95% = 16.9.

Figure 3.18. Chosen 60,000 square km sites where *Strumigenys* had high collection records.

Figure 3.19. Distance Decay of all *Strumigenys* species across the US using 28 chosen 60,000 km^2 regions. Model parameters, minimum specimen records per unit area = 20, iterations = 1000, Geographic area 60,000 sq km, for both models, $p < 0.0001$, $R^2 > 0.47$.

Figure 3.20. Distance Decay of Nearctic clade *Strumigenys* species across the US using 28 chosen 60,000 km^2 regions. Model parameters, minimum specimen records per unit area = 20, random draws of specimen records per replicate = 1000, iterations = 1000.

Figure 3.21. Distance Decay of species belonging to the Nearctic lineage across twelve 60,000 km^2 regions with at least 100 collection records (no duplicate collection record per species). Regions with the most abundant *Strumigenys* records are close together and the number and proportion of shared species does not decrease or increase with distance measured by Jaccard's Index.

Figure 3.22. Climate ranges occupied by *Strumigeny* species. Species origination estimated from range construction using collection records. Phylogenetic distance of ultrametric tree is in absolute genetic differences from loci recovered using RAD-seq methods.

Figure 3.23. United States Map of 6142 *Strumigenys* collection records colored by biogeographic origin.

Figure 3.24. Global climate records of all native and non-native *Strumigenys.* Global climate records (precipitation of driest quarter and mean annual temperature) obtained from collections show climatic ranges occupied both outside and within the US.

Figure 3.25. Nearctic climate records of all native and non-native *Strumigenys*. US collection records hightlighted and records outside the US faded, show US climates occupied by species occurring elsewhere fall within the ranges of climates occupied elsewhere, n = 9606. In the US, the cooler MAT ranges occupied by the Nearctic lineage also have the highest PDQ.

Figure 3.26. Global mean annual temperature records (°C) obtained from collection localities of species ranges of mean annual temperatures outside of the US. Ranges differ according to biogeographic lineage they belong to (ANOVA, $R^2 = 0.06$, Observations = 3464, $F = 1982.5$, $p = < 0.0001$).

Figure 3.27. Species occupy similar ranges in the US to those they occupy outside the US and differ according to lineage (see Table 1. Below).

Figure 3.28. Global precipitation of driest quarter (mm) records obtained from collection localities show ranges of precipitation of driest quarter. Ranges differ according to biogeographic lineage they belong to (ANOVA, $R^2 = 0.04$, Observations = 3464, $F = 50.1$, $p = < 0.0001$).

Figure 3.29. Species occupy similar but much narrower ranges in the US to those they occupy outside the US and differ according to lineage (see Table 2. Below).

3.8 List of Tables

Table 3.1. US Collection records show species of different biogeographic origins occupy different MAT environments. Each Pairs Wilcoxon Rank tests reveal that all lineages occupy different climatic ranges. Tests reveal whether lineages difference in climatic ranges (MAT) they occupied within the US. The ranges that species of lineages occupy within the U.S. falls within MAT ranges lineages occupy outside the U.S. These results are consistent with phylogenetic niche conservation and support the colonization assembly hypothesis.

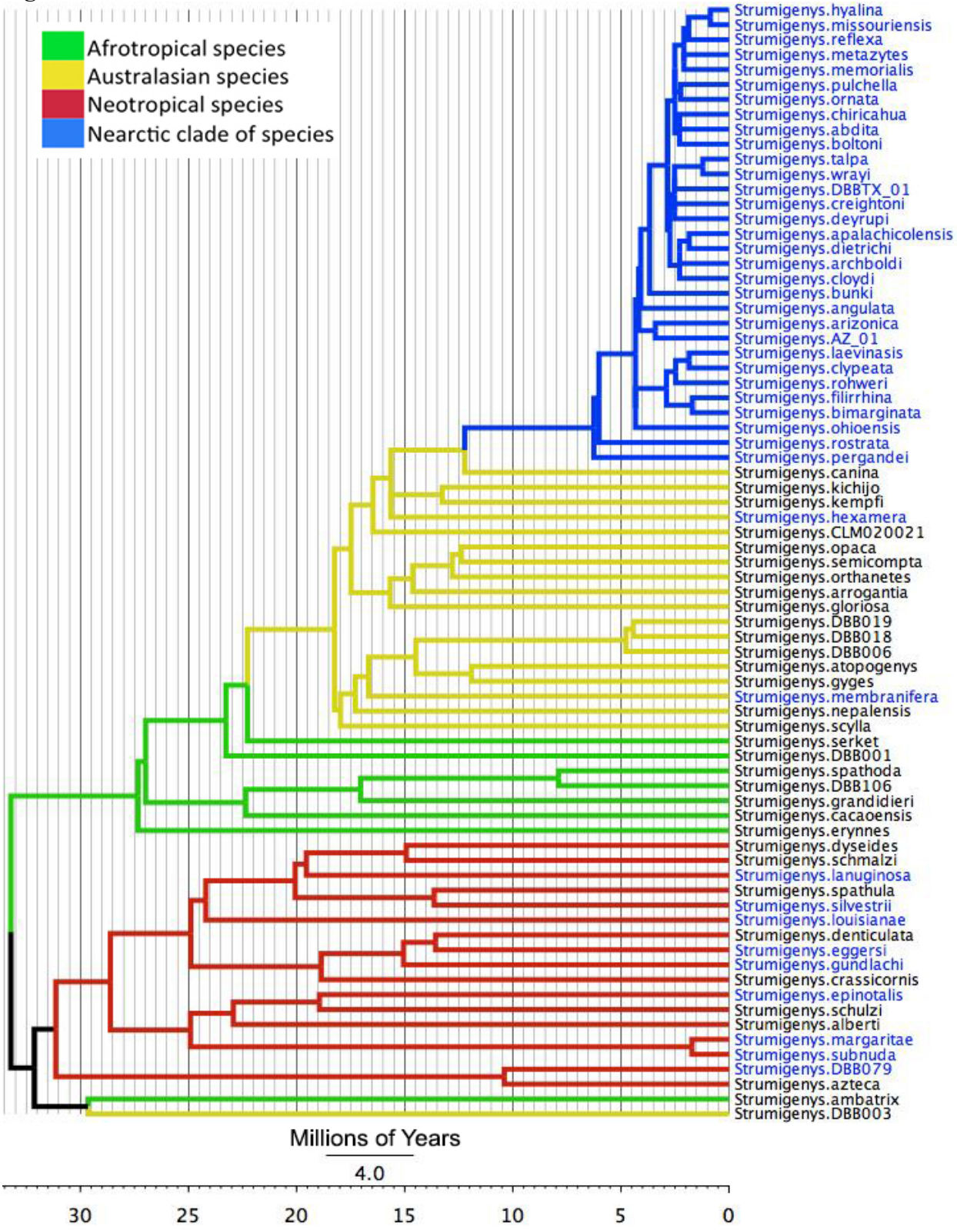
Table 3.2. US Collection records show species of different biogeographic origins occupy different PDQ environments. Each Pairs Wilcoxon Rank tests reveal that all lineages occupy different climatic ranges. Tests reveal whether lineages difference in climatic ranges (PDQ) they occupied within the US. The ranges that species of lineages occupy within the U.S. falls within PDQ ranges lineages occupy outside the U.S. These results are consistent with phylogenetic niche conservation and support the colonization assembly hypothesis.

Table 3.3. ANOVA Comparisons of PDQ and MAT environments within each of the 28 regions between tropical migrants and members of the Nearctic lineage. Table of ANOVAs testing for within site differences in Mean Annual Temperature (MAT, C°) and Precipitation in Driest Quarter (PDQ, mm) between climatic records obtained from collection records for species of Nearctic origin verses those obtained for species of tropical origin. In each regional site having greater than seven collection records of species from both Nearctic and Tropical origin (n=observations of records), species of tropical origin occurred in warmer and drier climates than

did species of Nearctic origin. These results are significant for 44% of sites tested for MAT and 50% of sites tested for PDQ differences. Though not significant in all sites, there is a general trend of higher MAT records (94% of sites) and lower PDQ records (67% of sites) for tropical species.

3.9 Figures and Tables

Figure 3.1.



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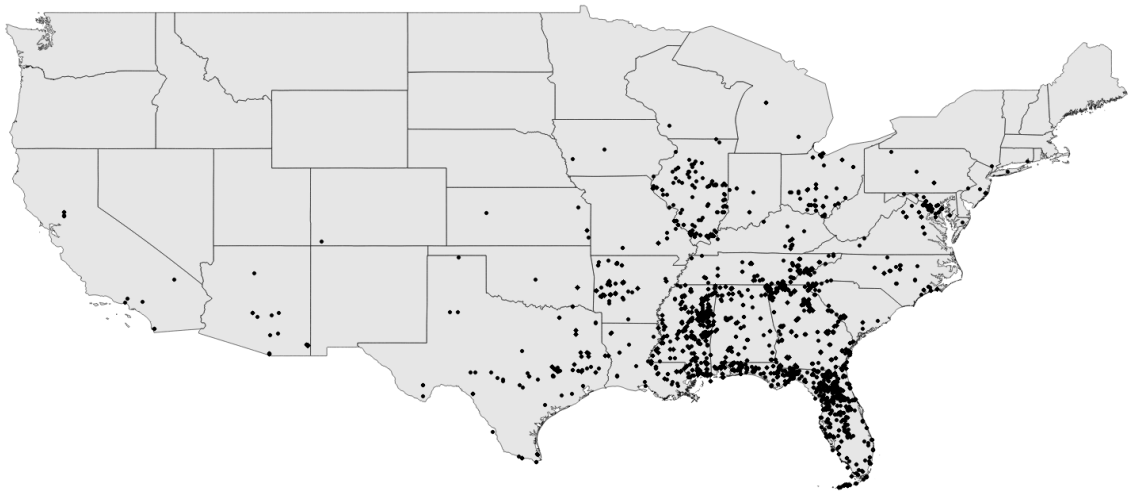

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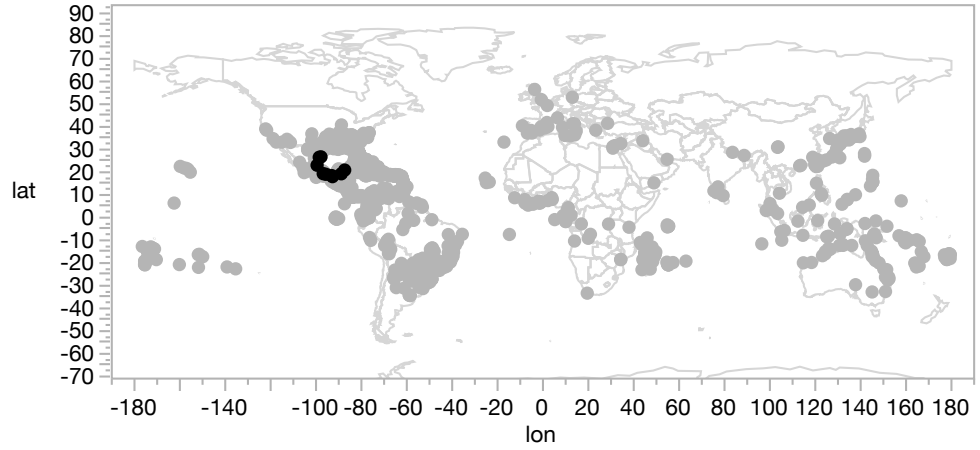

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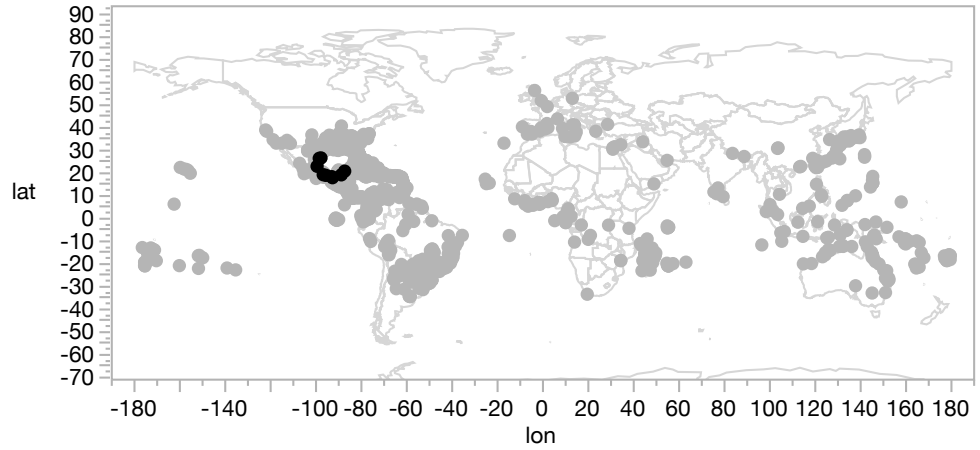

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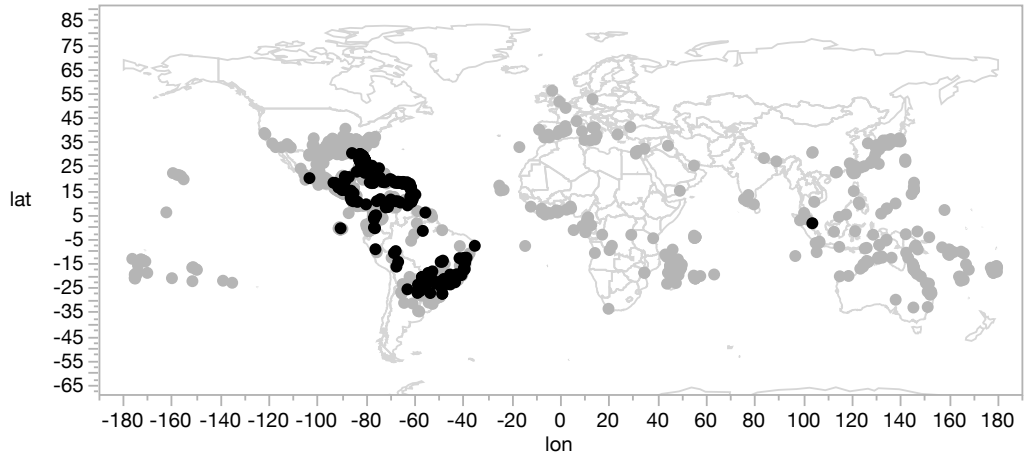

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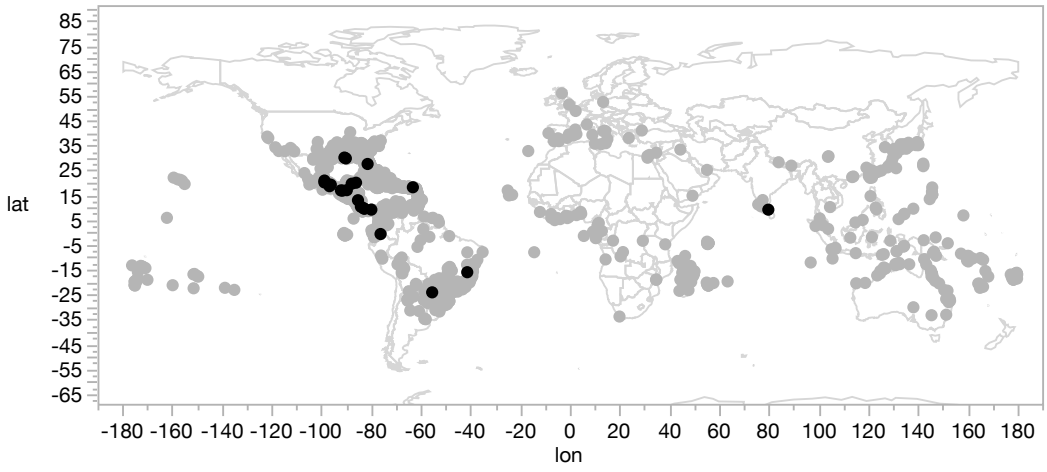

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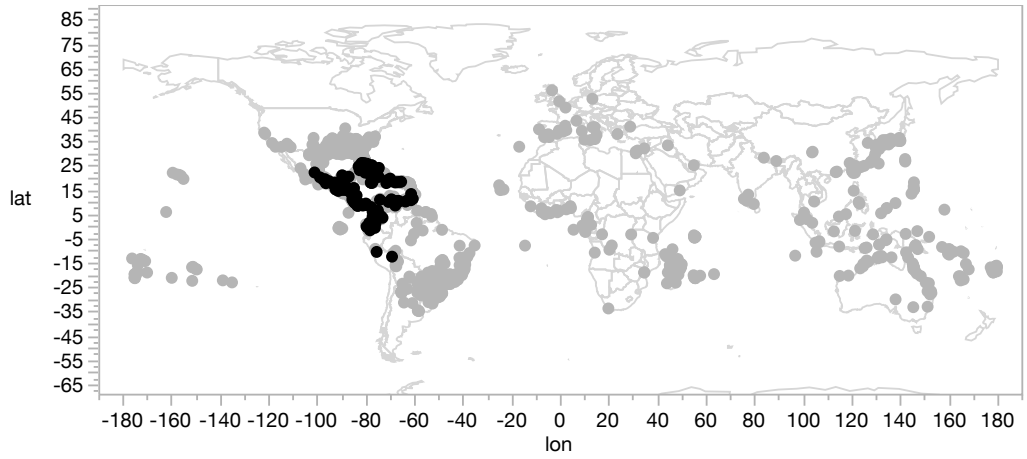
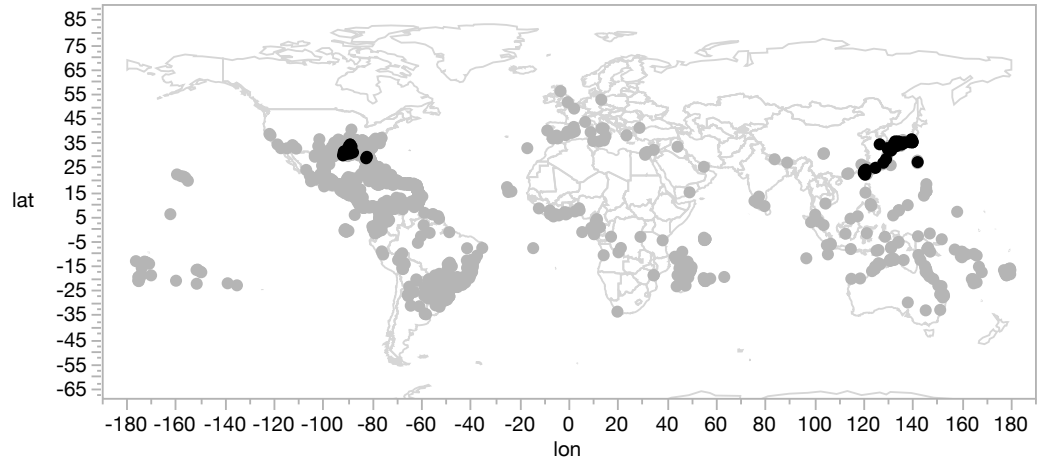


Figure 3.8.



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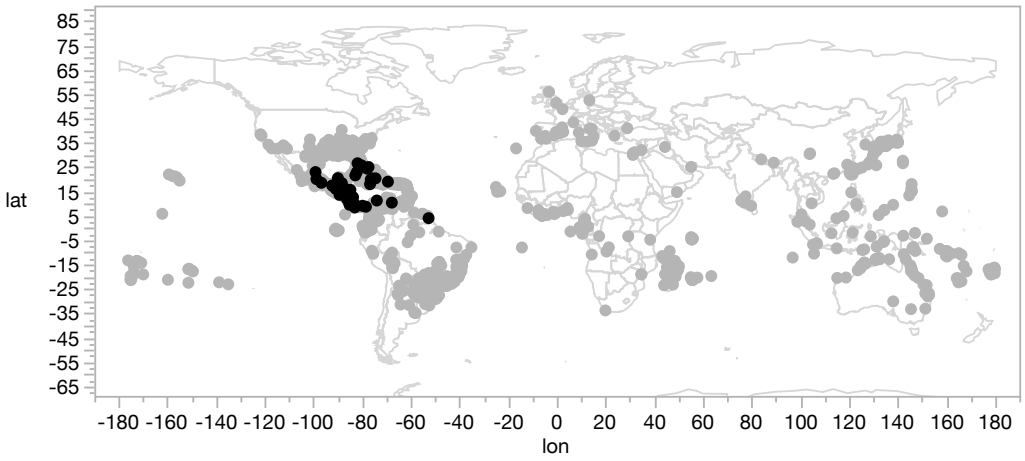

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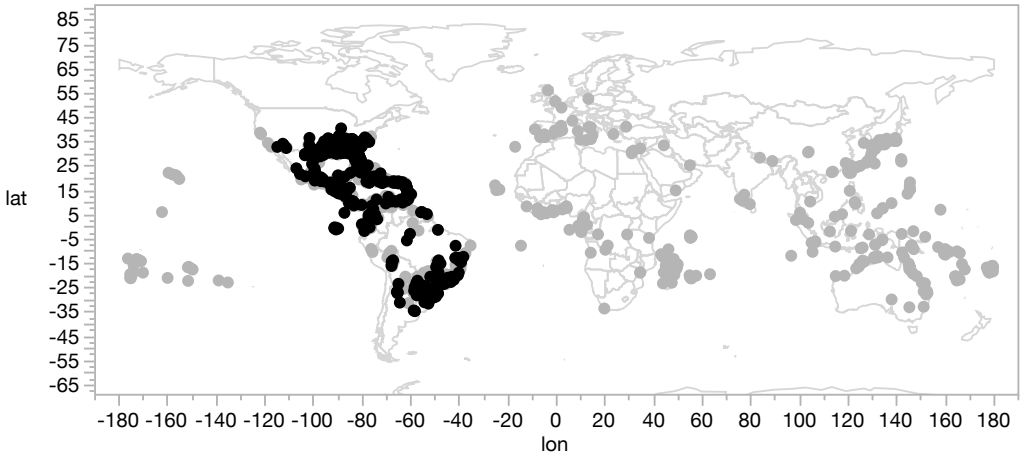

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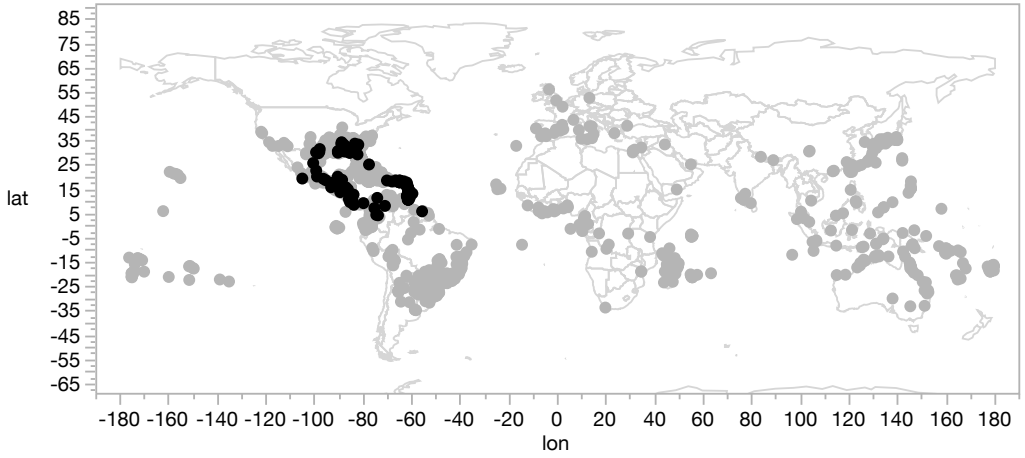

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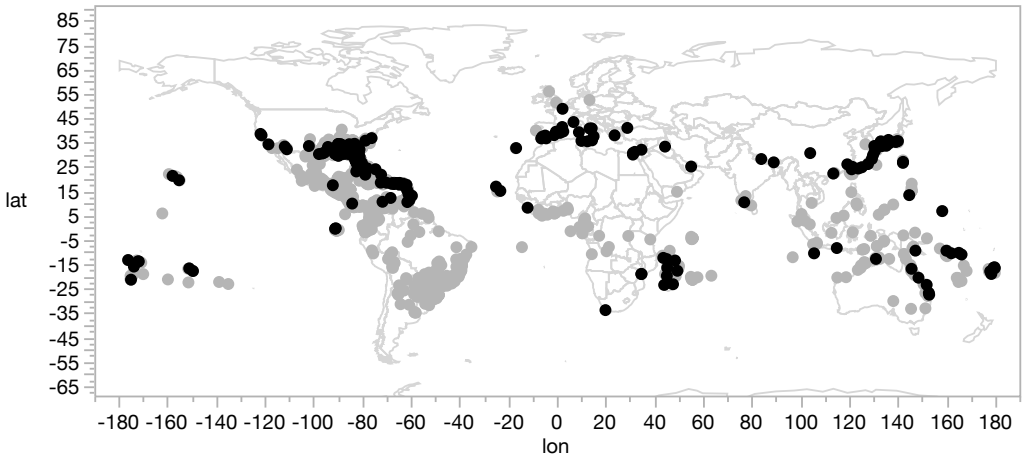

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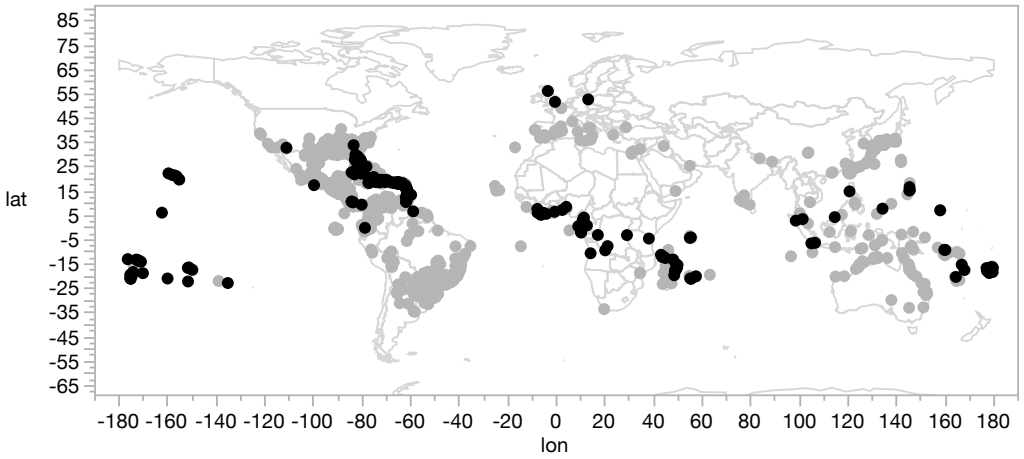

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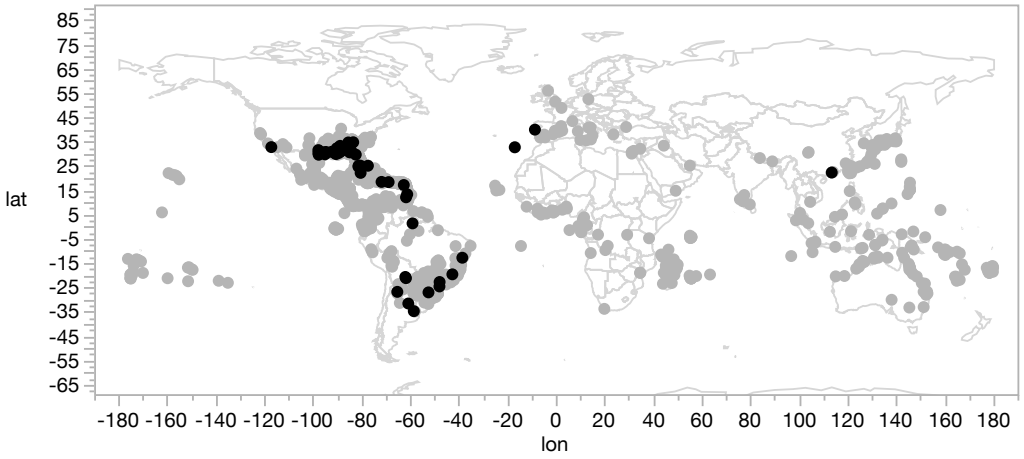

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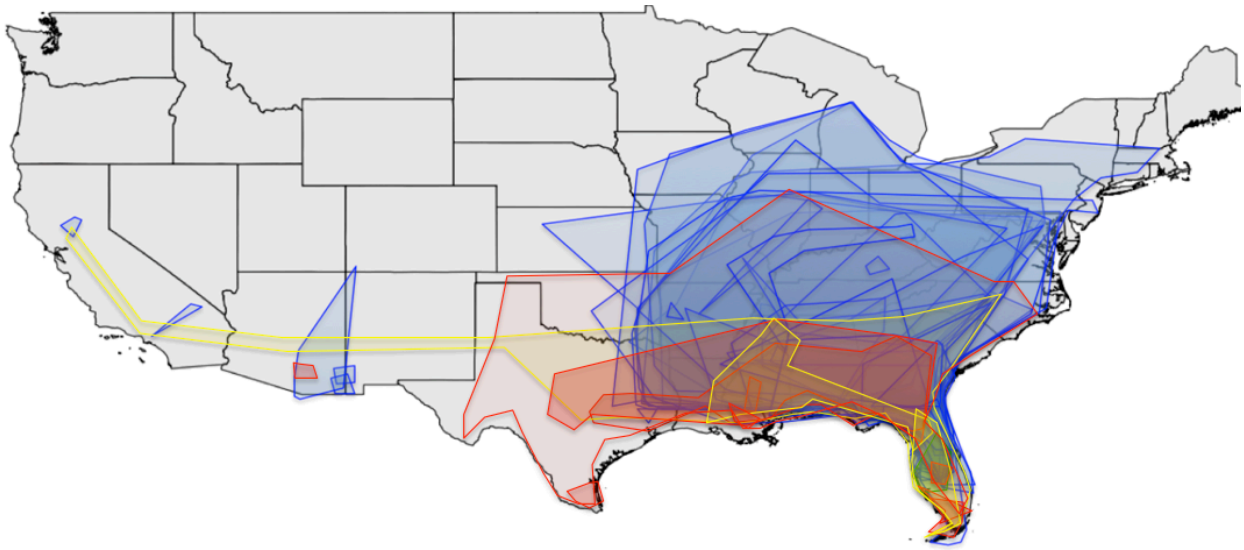

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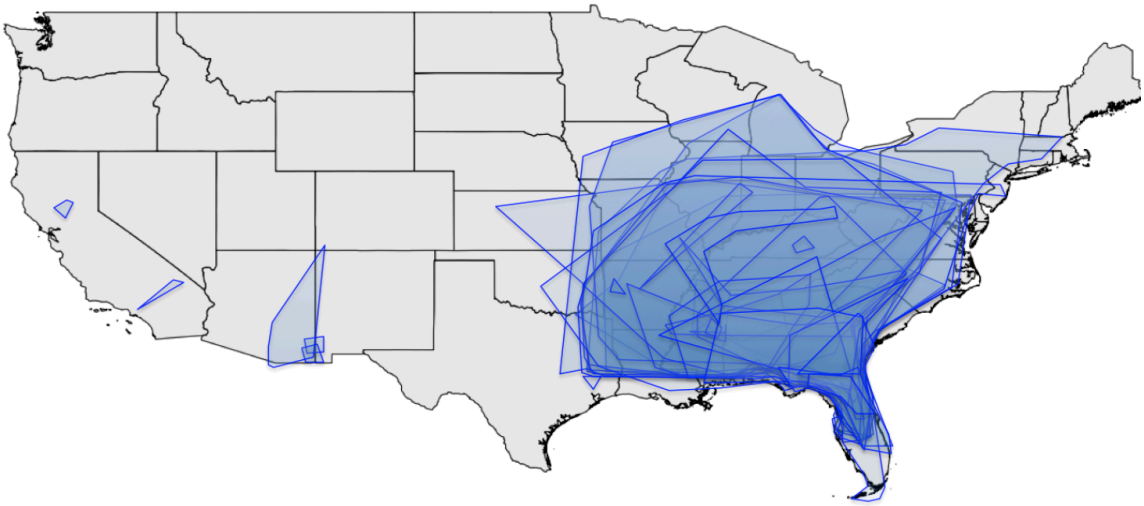

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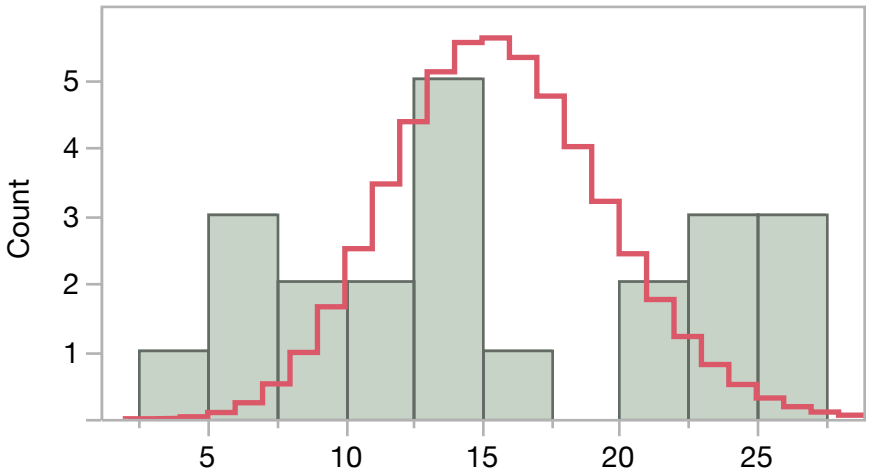

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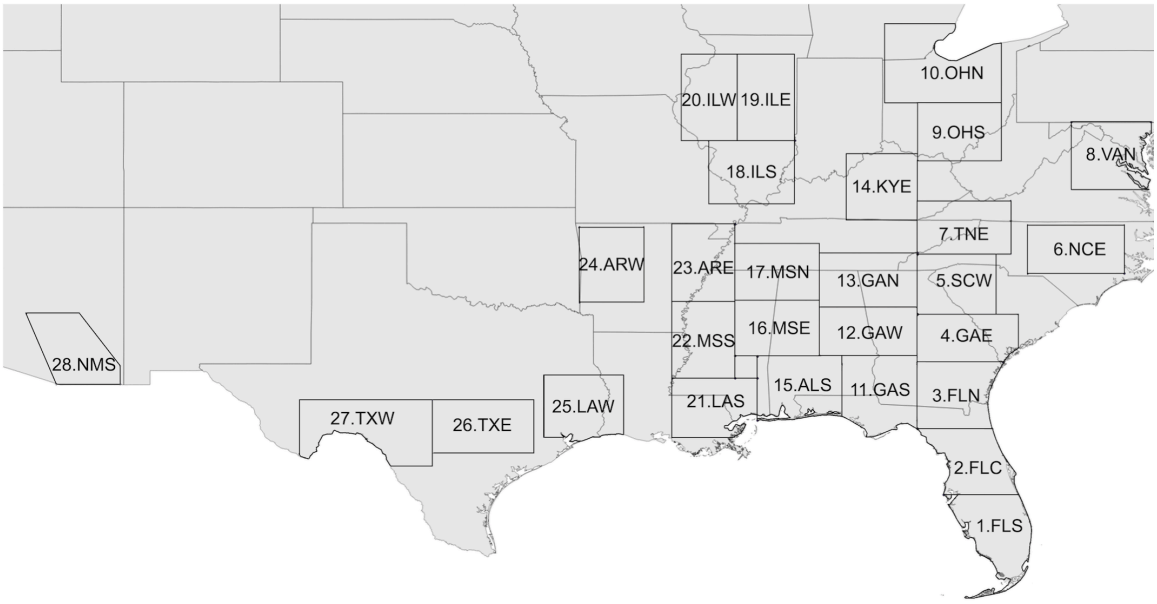

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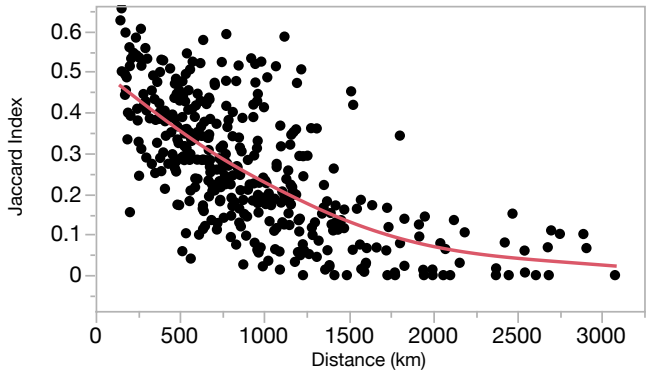

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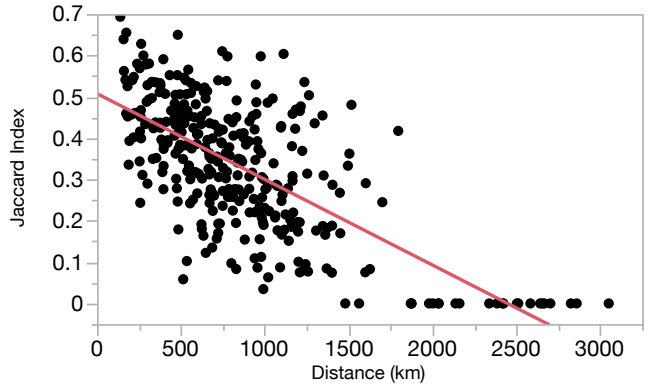
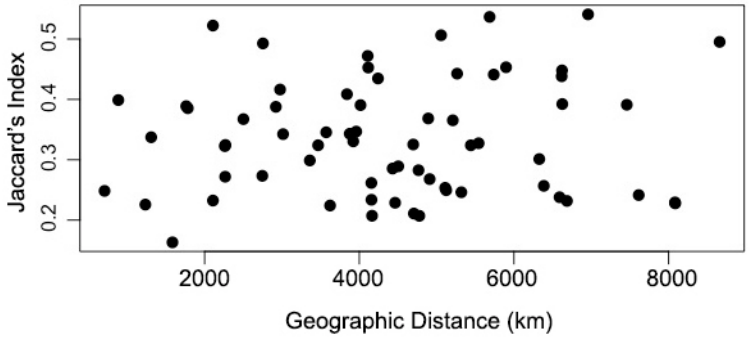


Figure 3.21.



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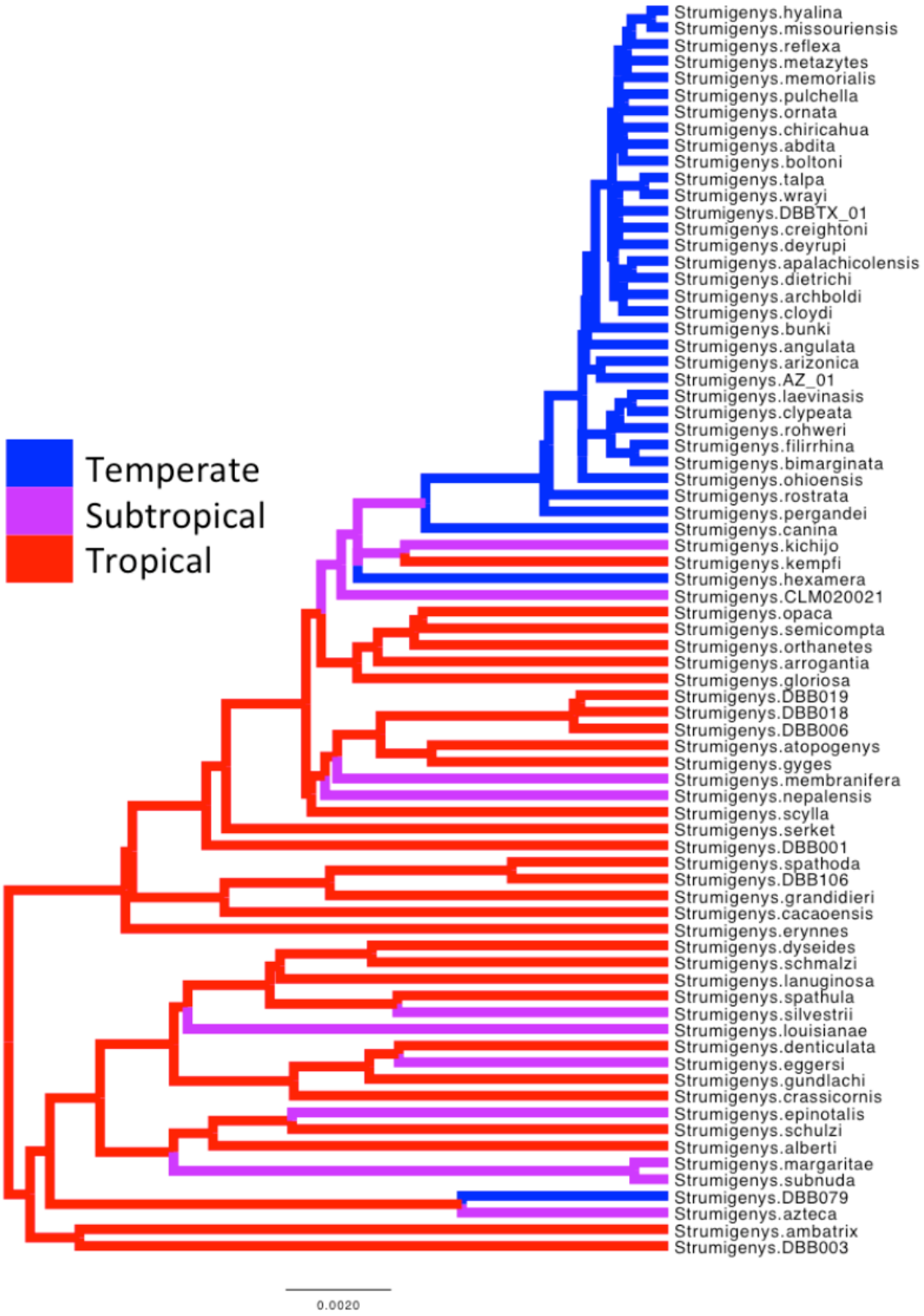
Temperate
Subtropical
Tropical
Strumigenys.hyalina
Strumigenys.missouriensis
Strumigenys.reflexa
Strumigenys.metazytes
Strumigenys.memorialis
Strumigenys.pulchella
Strumigenys.ornata
Strumigenys.chiricahua
Strumigenys.abdita
Strumigenys.boltoni
Strumigenys.talpa
Strumigenys.wrayi
Strumigenys.DBBTX_01
Strumigenys.creightoni
Strumigenys.deyrupi
Strumigenys.apalachicolensis
Strumigenys.dietrichi
Strumigenys.archboldi
Strumigenys.cloydi
Strumigenys.bunki
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Strumigenys.arizonica
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Strumigenys.laevinasis
Strumigenys.clypeata
Strumigenys.rohweri
Strumigenys.filirrhina
Strumigenys.bimarginata
Strumigenys.ohioensis
Strumigenys.rostrata
Strumigenys.pergandei
Strumigenys.canina
Strumigenys.kichijo
Strumigenys.kempfi
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Strumigenys.CLM020021
Strumigenys.opaca
Strumigenys.semicompta
Strumigenys.orthanetes
Strumigenys.arrogantia
Strumigenys.gloriosa
Strumigenys.DBB019
Strumigenys.DBB018
Strumigenys.DBB006
Strumigenys.atopogenys
Strumigenys.gyges
Strumigenys.membranifera
Strumigenys.nepalensis
Strumigenys.scylla
Strumigenys.serket
Strumigenys.DBB001
Strumigenys.spathoda
Strumigenys.DBB106
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Strumigenys.lanuginosa
Strumigenys.spathula
Strumigenys.silvestrii
Strumigenys.louisianae
Strumigenys.denticulata
Strumigenys.eggersi
Strumigenys.gundlachi
Strumigenys.crassicornis
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Strumigenys.schulzi
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Strumigenys.ambatrix
Strumigenys.DBB003
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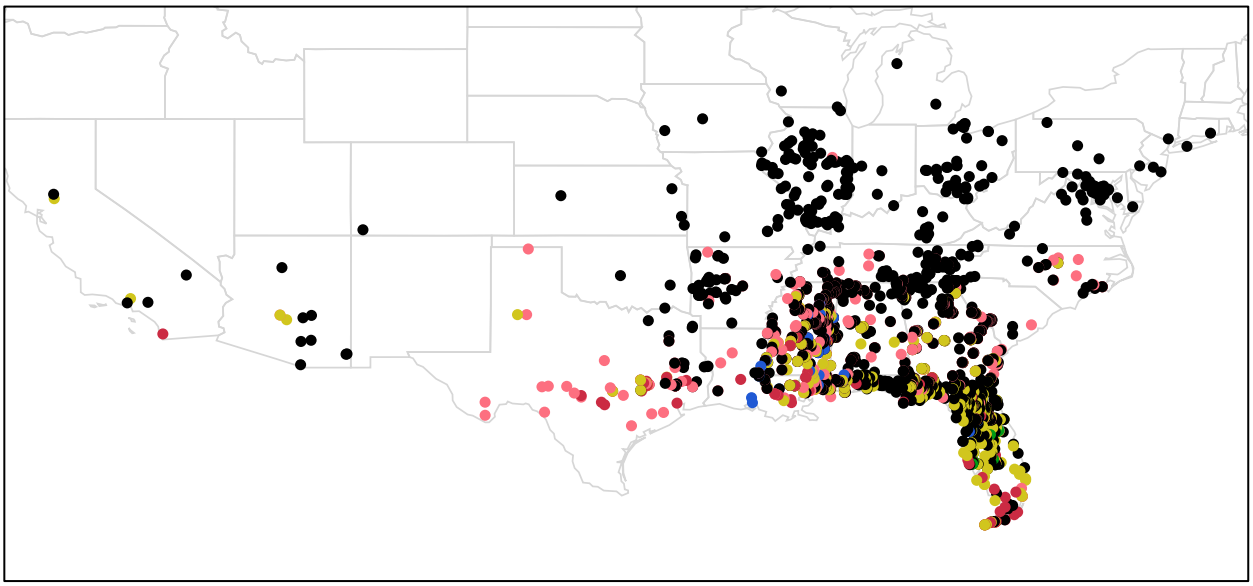
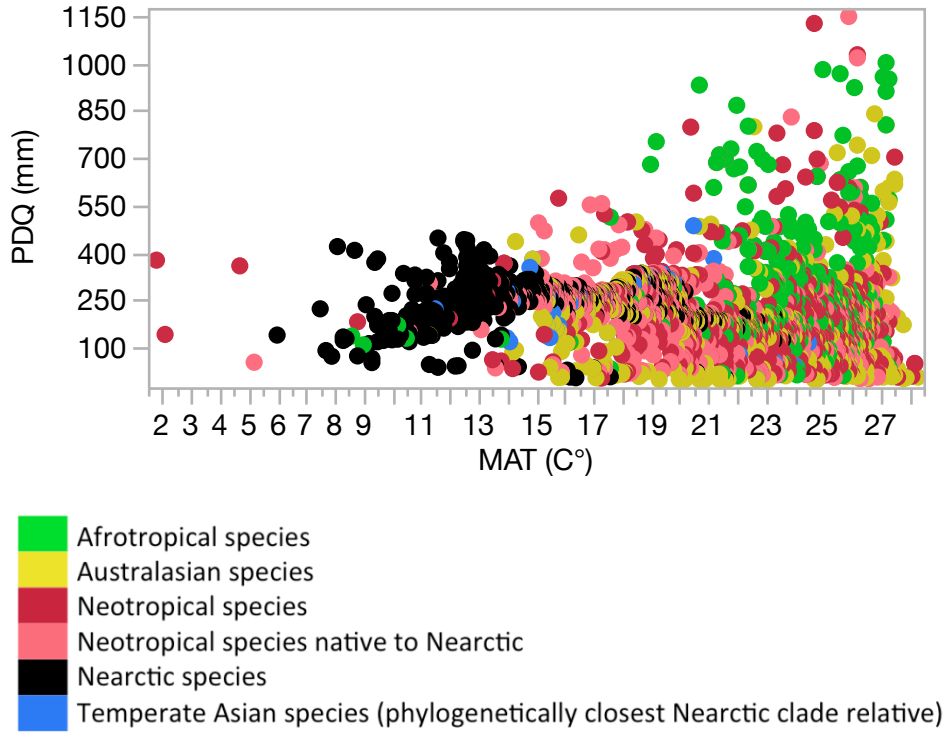
Figure 3.23.



Afrotropical species
Australasian species
Neotropical species
Neotropical species native to Nearctic
Nearctic species
Temperate Asian species (phylogenetically closest Nearctic clade relative)

Figure 3.24.



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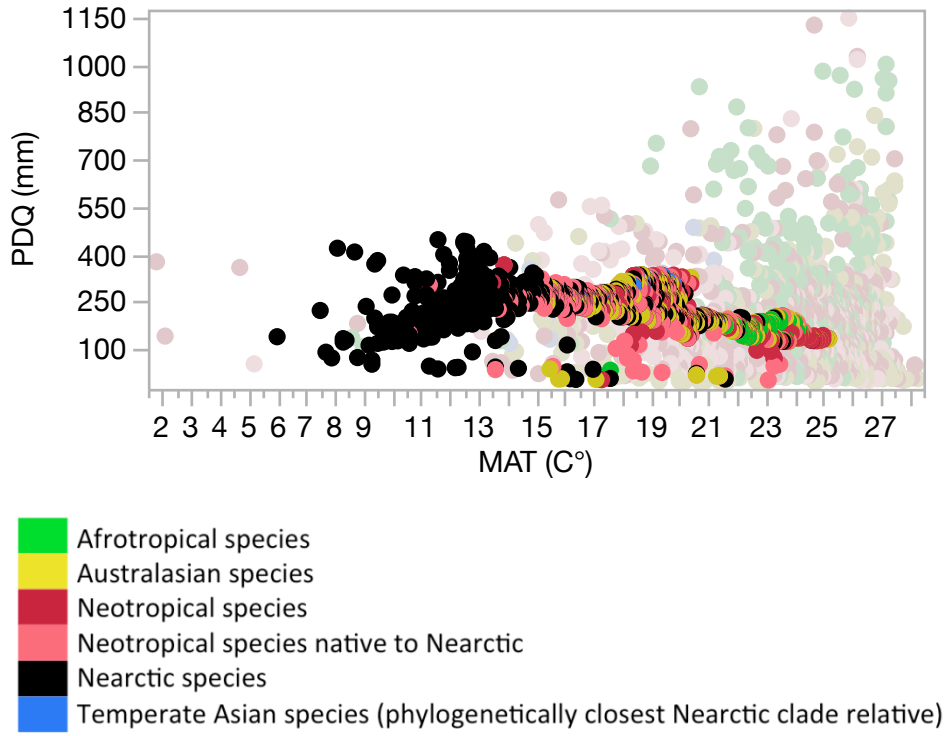

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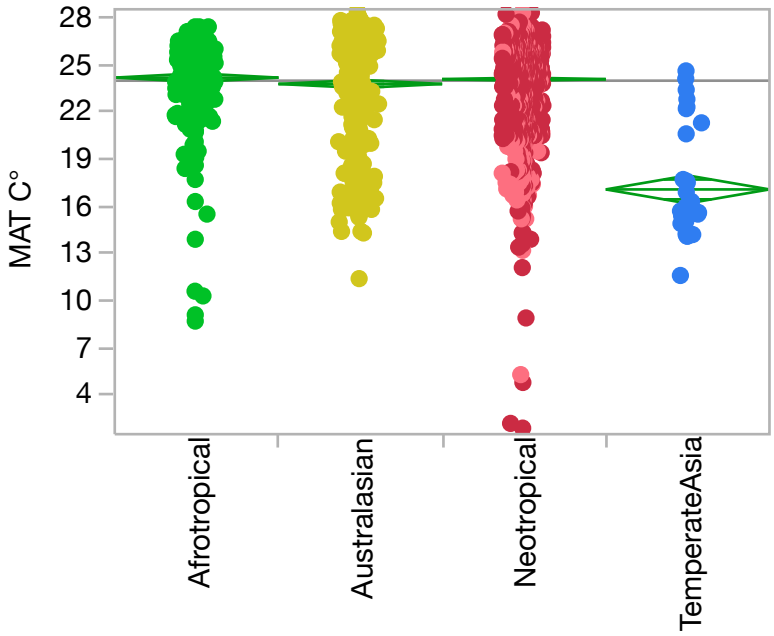

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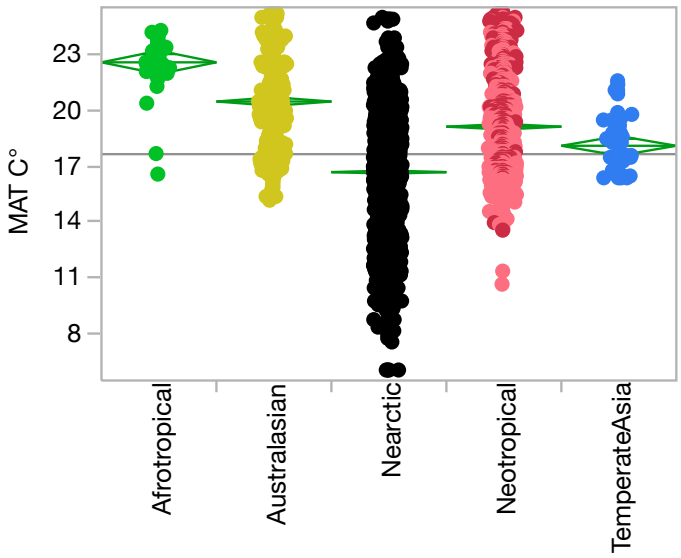
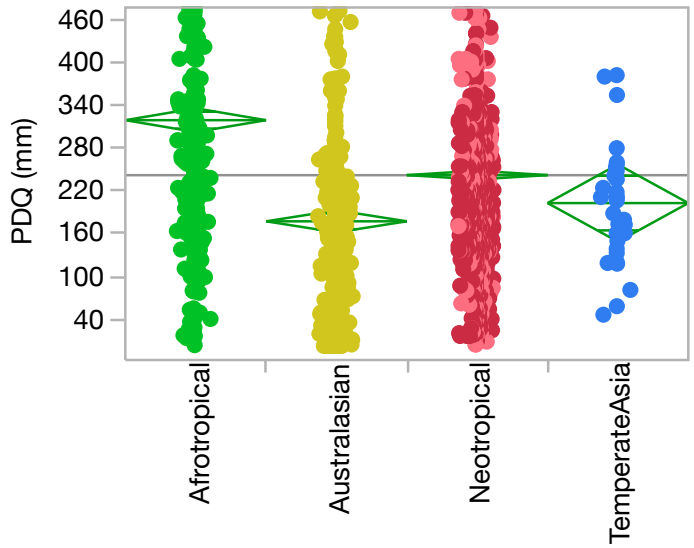


Figure 3.28.



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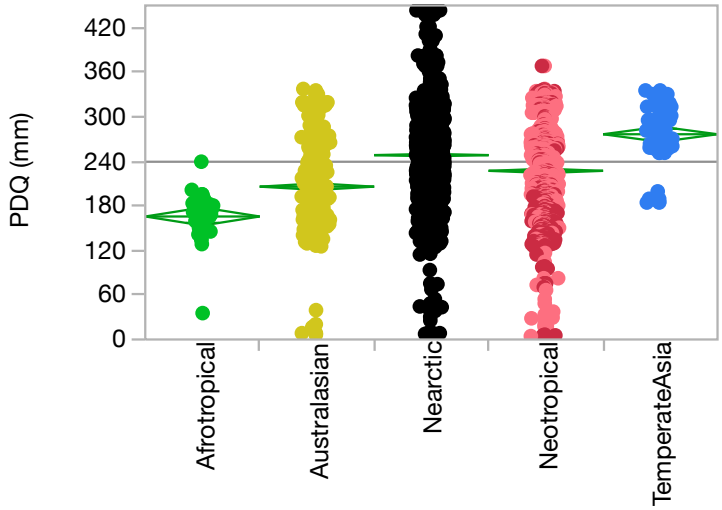

Table 3.1.

Annual Temperature Records for US collected Species

R^2 = 0.21, Observations = 6142, F = 422.74, p = <0.0001

Each Pairs Wilcoxon Rank test

Level	- Level	Difference	Std Err Dif	Lower CL	Upper CL	p-Value
Afrotropical	Nearctic	5.88	0.32	5.25	6.52	<0.0001
Afrotropical	TemperateAsia	4.47	0.42	3.65	5.29	<0.0001
Australasian	Nearctic	3.78	0.12	3.54	4.03	<0.0001
Afrotropical	Neotropical	3.45	0.33	2.81	4.09	<0.0001
Neotropical	Nearctic	2.43	0.09	2.26	2.61	<0.0001
Australasian	TemperateAsia	2.37	0.3	1.79	2.95	<0.0001
Afrotropical	Australasian	2.1	0.34	1.43	2.77	<0.0001
TemperateAsia	Nearctic	1.41	0.27	0.87	1.95	<0.0001
Australasian	Neotropical	1.35	0.14	1.08	1.62	<0.0001
Neotropical	TemperateAsia	1.02	0.28	0.47	1.58	0.0003

Table 3.2.

Precipitation Driest Quarter Records for US collected Species

One Way ANOVA, R^2 = 0.09, Observations = 6142, F = 147.72, p = <0.0001

Each Pairs Wilcoxon Rank test

Level	- Level	Difference	Std Err Dif	Lower CL	Upper CL	p-Value
TemperateAsia	Afrotropical	110.8	8.1	94.9	126.8	<0.0001
Nearctic	Afrotropical	82.7	6.3	70.4	95	<0.0001
TemperateAsia	Australasian	70.6	5.7	59.4	81.8	<0.0001
Neotropical	Afrotropical	61.5	6.4	49	74	<0.0001
TemperateAsia	Neotropical	49.3	5.5	38.6	60	<0.0001
Nearctic	Australasian	42.5	2.4	37.8	47.3	<0.0001
Australasian	Afrotropical	40.2	6.6	27.3	53.2	<0.0001
TemperateAsia	Nearctic	28.1	5.3	17.6	38.5	<0.0001
Neotropical	Australasian	21.3	2.7	16	26.6	<0.0001
Nearctic	Neotropical	21.2	1.7	17.9	24.6	<0.0001

Table 3.3.

Site	MAT	MAT diff.	n	Lineage	R	F	p	PDQ	PDQ diff.	R	F	p
ALS	18.81	0.11	203	Nearctic	0.1	2.1	0.1482	302.3	4.2	0.0	3.5	0.0646
ALS	18.92		106	Tropical				306.5				
ARE	16.08	0.08	23	Nearctic	0	1	0.32	250.9	-2.4	0.1	2.4	**0.013**
ARE	16.16		19	Tropical				248.5				
ARW	15.00	0.30	148	Nearctic	0.1	2.1	0.14	280.7	-9.8	0.1	0.7	0.39
ARW	15.30		9	Tropical				270.9				
FLC	20.87	0.32	394	Nearctic	0.1	44.8	**0.0001**	190.6	-7.4	0.1	57.2	**0.0001**
FLC	21.19		356	Tropical				183.2				
FLN	19.69	-0.08	200	Nearctic	0.1	1.9	0.18	206.2	0.4	0.0	0.2	0.67
FLN	19.61		81	Tropical				206.6				
FLS	22.64	0.67	108	Nearctic	0.1	48.4	**0.0001**	150.0	2.1	0.0	0.9	0.33
FLS	23.31		391	Tropical				152.1				
GAE	17.69	0.15	234	Nearctic	0	8.1	**0.0047**	218.9	-3.4	0.0	9.5	**0.0022**
GAE	17.84		74	Tropical				215.5				
GAN	14.27	0.43	293	Nearctic	0	3.1	0.08	298.6	-11.4	0.0	3.9	**0.05**
GAN	14.70		12	Tropical				287.2				
GAS	19.45	0.00	180	Nearctic	0	0	0.95	263.2	-5.3	0.0	13.9	**0.0002**
GAS	19.45		138	Tropical				257.9				
GAW	16.63	0.18	90	Nearctic	0	3.6	0.06	250.5	-4.7	0.0	2.1	0.15
GAW	16.81		52	Tropical				245.8				
LAS	19.02	0.27	57	Nearctic	0.1	11.6	**0.0008**	316.0	1.2	0.0	0.7	0.41
LAS	19.29		104	Tropical				317.2				
LAW	18.79	0.25	63	Nearctic	0.1	9.5	**0.0028**	265.7	3.3	0.0	0.4	0.52
LAW	19.04		23	Tropical				269.0				
MSE	16.85	0.02	629	Nearctic	0	0.6	0.44	262.3	-1.4	0.0	16.3	**0.0001**
MSE	16.87		246	Tropical				260.9				
MSN	15.79	0.06	192	Nearctic	0	0.6	0.45	261.5	-1.2	0.0	0.7	0.4
MSN	15.85		43	Tropical				260.3				
MSS	17.38	0.09	115	Nearctic	0	1.2	0.28	255.5	1.1	0.0	0.2	0.68
MSS	17.47		75	Tropical				256.6				
NCE	15.05	0.34	41	Nearctic	0.2	16	**0.0002**	251.1	-10.3	0.4	34.7	**0.0001**
NCE	15.39		16	Tropical				240.8				
NMS	14.20	6.44	14	Nearctic	0.7	35.9	**0.0001**	38.2	-18.9	0.6	33.1	**0.0001**
NMS	20.64		7	Tropical				19.3				
SCW	15.56	0.56	357	Nearctic	0	9.9	**0.0018**	292.9	-28.0	0.0	11.4	**0.0008**
SCW	16.12		54	Tropical				264.9				

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4. Chapter 4. Assembly of Nearctic *Strumigenys*: Interpreting Patterns and Processes from Meta-Communities to Microsites.

4.1 ABSTRACT

Processes that create patterns in biodiversity and community species composition differ as a function of spatial scale, phylogenetic relationship, and trait similarities and differences. However, few studies have applied the same set of community ecology hypotheses to examine these relationships at very different spatial scales. I examined the phylogenetic and trait relationships of co-occurring *Strumigenys* species at very large to very small geographic spatial scales to test predictions of a competition hypothesis against three alternative hypotheses - habitat filtering, phylogenetic niche conservation, and evolutionary adaptation. The competition hypothesis is that species with more similar in traits are more likely to compete for shared resources, potentially resulting in micro or macro allopatry in which species with more similar traits avoid each other. An alternative to the competition hypothesis is the hypothesis of evolutionary adaptation, which is that more closely related species occur in dissimilar environments. A finding of micro allopatry between closely related species and micro sympatry of distantly related species would support the competition hypothesis. However, finding a lack of micro allopatry at small spatial scales but allopatry at larger spatial scales would support the evolutionary adaptation hypothesis. The hypothesis of habitat filtering and phylogenetic niche conservation are not mutually exclusive. The hypothesis of habitat filtering is that species with more similar traits will co-occur in similar environments to which their shared traits adapt them. The hypothesis of phylogenetic niche conservation is that phylogenetically more closely related species are more likely to co-occur due to shared evolutionary histories.

I evaluated *Strumigenys* species co-occurrences in relation to these four hypotheses on spatial scales ranging from twenty-eight 60,000 km^2 bioregions across the United States to much smaller areas within the southeastern United States, including communities of *Strumigenys* inhabiting 02.0 ha areas, to local communities occupying areas of 25 m^2, and finally, to the smallest spatial scale of 0.10 m^2 microsites. The smallest scales are still relevant because these ants are very small (< 2.5mm) and workers forage within a few tens of cm from the nest site. This is the first such study to test the same set of community ecology hypotheses across this range of spatial scales. The phylogeny reveals that the *Strumigenys* species in the United States are either endemic to North America or are immigrants and represent more distantly related phylogeographic regions. I tested the consistency of patterns of co-existence expected with the hypotheses of competition, evolutionary adaptation, environmental filtering, and phylogenetic niche conservation at each geographic scale. In performing these tests, I either included all *Strumigenys* species occurring at a given spatial scale, or include only endemic species of Nearctic origins. At all geographic scales larger than 0.10m^2 microsites, from 25m^2 local communities to 60,000km^2 bioregions across the United States, occurrence patterns supported the hypotheses of phylogenetic niche conservation and habitat filtering. At no geographic or phylogenetic scale are patterns consistent with the competition hypothesis, that either past or present competition structures Nearctic *Strumigenys* communities. At the largest scale of 60,000km^2 bioregions, patterns of species diversity were consistent with a prediction of niche conservation, that species will occupy more similar environments to those of closely related lineages; and species occupy bioregions with current climatic ranges that are more similar to those of their closest related lineage. Species belonging to lineages of tropical origins occupied warmer climatic regions and those of Nearctic origins occupied cooler climatic ranges. In 0.20 ha

communities, *Strumigenys* communities co-varied with tree communities and more species tended to occur in the same 0.20 ha area, supporting habitat filtering. In local $25m^2$ communities, more closely related species tended to occupy more similar nest sites, supporting predictions of both habitat filtering and niche conservation. At the smallest scale of $0.10m^2$ microsites, *Strumigenys* show no phylogenetic structure, no associations with microenvironments, and co-occurrence cannot be distinguished from random, a result that is either due to a lack of interactions, or an artifact of small sample size as microsites had very few species on average.

4.2 INTRODUCTION

Inferring what processes maintain biological diversity from observing patterns of diversity is highly dependent on the spatial scale on which one studies these processes (Chave 2013). Ecological processes act differently on different spatial scales and one can easily misinterpret the importance of an ecological process by only investigating it on a single spatial scale (Levin 1992, Campos, Vasconcelos et al. 2011, McGarigal, Wan et al. 2016). Despite the importance of ecological process studies across multiple spatial scales, there are still relatively few studies that address scale dependence of such processes. A recent review of more than 800 ecology papers found less than 5% of papers modeling habitat selection, and less than 25% of multi-scale habitat studies, assessed scale dependent patterns and processes (McGarigal, Wan et al. 2016). In the case of ant communities, there is a long history and large body of work investigating community assembly, but few studies encompass scales from biogeographic regions to local communities. Those that do, have never investigated local communities at a scale below $1m^2$ (Kaspari, Yuan et al. 2003). The importance of the present multi-scale study is that it allows one to assess how ecological processes operate at different spatial scales.

Biogeographic regions are not a typical scale to carry out investigations of community assembly. The reason is that ecological communities rarely cover biogeographic spatial scales. However, understanding the origins of a pattern at one geographical scale can help understand processes that structure patterns below and above that scale (Gotelli and Ellison 2002, Kneitel and Chase 2004, Manfrin, Traversetti et al. 2016). Because the importance of stochastic, biotic, or abiotic processes shaping biological patterns may strengthen or weaken as a function of geographic scale, studies focusing on organizing processes at large and small geographic scales are necessary to understand how biological systems self assemble (Levin 1992, Rahbek 2005, Palmer 2006, Chave 2013). Because biotic interactions among species cannot act across large distances, local scales are where interspecific interactions have any scope for being important. Conversely, abiotic factors *e.g.* geographic barriers, can operate on any spatial scale, and potentially can define species ranges at large geographic scales (Levin 1992). Other factors, such as environmental heterogeneity, may also occur at all scales and also affect diversity patterns at all scales (Stein, Gerstner et al. 2014).

A goal of community ecology is to determine to what degree communities are composed of closely related species that share phylogeographic histories or are dispersal assembled and composed of more distantly related migrants. Understanding how communities are assembled is facilitated not only by understanding the phylogenetic relationships of species, but also their phylogeographic histories as well. Where species evolved, when species migrated to their current location, and where species were when they evolved traits are all necessary information to disentangle biotic from abiotic evolutionary forces shaping contemporary community structure (Pearse, Jones et al. 2013). I used our previously reconstructed globally represented *Strumigenys*

phylogeny to describe the evolutionary relationships and infer biogeographic histories of *Strumigenys* species (Chapter 3).

Over the last decade, there has been an explosion of research testing whether communities of trophically similar organisms are random phylogenetic assemblages of species or not (Cavender-Bares, Ackerly et al. 2004, Ulrich and Gotelli 2010, Ulrich, Piwczynski et al. 2012, Ulrich and Gotelli 2013). Do communities consist of more closely or less closely related species than expected from a random sample of species from the available species pool? Most such studies are of plant communities, but the logic applies also to animal communities and geographic patterns of animal diversity. I use collections records from museums, published records, or those I collected for this study to estimate the available species pool of each geographic spatial scale. If *Strumigenys* geographic and environmental ranges overlap and species are more closely related than expected, one can conclude that they are phylogenetically conserved and environments filter species with traits conferring success in similar habitats so that species occupy similar geographic and environmental ranges. Conversely, if species with overlapping ranges are more distantly related than expected, habitats filter species with traits conferring success in those environments and co-occurring species likely evolved those traits *e.g,* physiological tolerance to freezing conditions, in different geographic areas of similar environments. This suggests assemblages are dispersal assembled and supports predictions of habitat filtering. To investigate whether competition or evolutionary adaptation drove this pattern, one would need to investigate species co-occurrence at a smaller scale where species potentially interact. Species co-occurring in large areas might not co-occur in smaller areas and therefore might not compete. If colonies of co-occurring *Strumigenys* have overlapping foraging territories, they are likely to interact. Colony interactions are most probably occurring in 0.10 m^2 microsites. If co-occurring species

are phylogenetically over-dispersed, this may be due to both past competition-driven niche differentiation and habitat filtering. On the other hand, if the pattern of phylogenetic over-dispersion disappears at smaller spatial scales, co-occurring species are likely filtered by habitats and climate, and competition would not be invoked to account for their large-scale over-dispersion. However, competition is potentially important if over-dispersion is observed in local community assemblages.

I used Mantel tests, tests of co-occurrence distributions, and Ulrich's *Niche* model to test which if any of the competing community assembly hypotheses are consistent with the observed patterns of species occurrences over local to biogeographic spatial scales (Ulrich, Piwczynski et al. 2012).

The importance that competition may play in determining which species can or cannot co-occur in ecological communities has had a long and contentious history in ecology (Case and Gilpin 1974, Schoener 1982, Connell 1983). The competition hypothesis says that species must have sufficient niche differences to co-exist, and that these niche differences will be manifest in morphological, physiological, or behavioral traits that promote co-existence. These trait differences can arise either by separate evolutionary trajectories that did not involve past competitive interactions, or as a result of niche divergence over periods of chronic competitive interactions among species. Competition experiments, mainly in laboratory microcosms, have provided support for predictions of competition theory (Gause 1932, Case and Gilpin 1974); and in these experimental settings, there is abundant research showing species can be made to compete with one another (Gurevitch, Morrow et al. 1992). Competition experiments in controlled lab environments often exhibit stronger competitive effects than in free-roaming

organisms (Gurevitch, Morrow et al. 1992). Examining a competition hypothesis over large and small spatial scales using field observations will help determine if competition among *Strumigenys* species in nature is important at any spatial scale. If so, this multi-spatial scale analysis will reveal at what spatial scale(s) competition influence(s) community assembly among a community of free-roaming *Strumigenys*.

Competition, deemed the "hallmark" of ant ecology, has also been the focus of much ant community research (Savolainen and Vepsalainen 1988, Andersen 1992, Alinvi, Bohlin et al. 2008, Cerda, Arnan et al. 2013, Fayle, Eggleton et al. 2015, Camarota, Powell et al. 2016, Ellwood, Bluthgen et al. 2016). Most studies of competition in ant communities have been conducted at small spatial scales, scales on which interactions are likely. However, these studies have rarely documented cases of competitive exclusion that lead to spatial segregation of species at larger spatial scales. If I observe, for example, a "checkerboard" pattern of species, such a pattern could reflect an underlying competition-driven community assembly process. Here I test whether competition or alternative community assembly hypotheses, environmental filtering, phylogenetic niche conservation, or evolutionary adaptation, better explain patterns of distribution and co-occurrence of Nearctic *Strumigenys*. Species in this genus of predatory ants overlap nearly completely in their Collembola diet, so a reasonable expectation is that competition will be a major community organizing process on local spatial scales (Wilson 1953, Dejean 1985, Dejean 1986, Bovet, Dejean et al. 1989). I use climate records and other environmental variables measured at collection localities of *Strumigenys* to characterize environments and to test the extent of species overlap in environment and/or geography over a range of geographic scales. There is no evidence of competition driven biogeographic range patterns in *Strumigenys* (Wiens 2011). The ranges of Nearctic *Strumigenys* species tend to

overlap widely (Chapter 3). Even so, competition may still drive local patterns of co-occurrence in species with overlapping ranges and competition therefore remains a focal hypothesis of this study.

Since the literature on ant communities has primarily focused on competition as the organizing process on local scales (Ribas and Schoereder 2002, Cerda, Arnan et al. 2013), the presumption of this study is that competition also organized *Strumigenys* ant communities. Choosing an appropriately small spatial scale to test predictions of the competition hypothesis against alternative assembly hypotheses is particularly important when investigating extremely small taxa with limited mobility. At each spatial scale, assumptions of interactions must be inferred from the life histories of species belonging to the focal community. Biologically important spatial scales divide into four categories. (1) Meta-communities are communities at the broadest scale include the entire geographic ranges of species belonging to a defined community over an entire ecological range. I define the meta-community as all *Strumigenys* species occurring in the United States. (2) Regional communities are communities within a meta-community that occupy an area larger than the species are likely to disperse across and entirely colonize over a generation. I define regional communities as 60,000 km^2 bioregions. Because bioregions are so large, it is unlikely any two colonies of *Strumigenys* would come into contact with each other and therefore interactions between colonies of different species in a regional community are infrequent or rare. (3) Local communities are collections of potentially interacting species within a relatively small area. Local communities lie within a regional community, and in this local regional community, all species within that community are able to disperse and fully colonize within a generation. Potential interactions in a local community are increasingly probable with decreasing scale. I investigate local communities at two spatial scales, local 0.20 ha areas and

$25m^2$ local communities. (4) Micro-sites are the smallest spatial scale, a scale on which species will often encounter each other during the period of co-occurrence. I define our microsites as $0.10m^2$ microsites. This is a scale appropriate for *Strumigenys* ants that are less than 3mm in length and often nest in an area the size of an acorn. However this scale may be too small for many ant communities because this area could not contain even a single colony of most larger ant species. Although these terms are not operational in terms of what are actually (or can actually be) measured, I focused on small spatial scales of local communities and microsites where interactions of competition would be most apparent if they are important to *Strumigenys* community assembly.

It is also necessary to define the trophic and phylogenetic scale of our focal community. If species of a community occupy different trophic levels, or have non-overlapping diets on the same trophic level, significant interactions are less likely, unless they involve competition for non-food resources. Moreover, if species are phylogenetically only distantly related, they may not share phylogeographic evolutionary histories. Without the potential to interact, either currently or over geologic time, one cannot test whether biotic interactions influence species assemblages. Trophic and phylogenetic scales can be combined to define four scale types. (1) All the organisms living in the same place (multiple trophic levels, no phylogenetic constraint) *e.g.* all the plants and animals in a tropical dry forest. (2) A trophically similar group of species likely to interact (diet overlap on the same trophic level, phylogenetically constrained by trophic level) *e.g.* All the tropical plants in a defined place. (3) A group of closely related organisms likely to interact *e.g.* direct competition of predation of one trophic level on another (single or multiple trophic level, phylogenetically constrained) *e.g.* All the ants (all ants are not trophically alike) living in a defined place. (4) A group of trophically similar closely related set of organisms

likely to interact (phylogenetically constrained, single trophic level); *e.g.* all the seed harvesting *Pogonomyrmex* ants living in a defined place where they are likely to interact. *Strumigenys* communities belong to the fourth scale, they overlap nearly completely in diet and are a monophyletic taxon of fairly recent origination (< 40 mya).

Strumigenys are the third most species-rich ant genus in the world. They are small (most around 2 mm) and cryptic, often escaping notice even by trained myrmecologists, yet they are abundant top predators of the brown food web (detritivores and those animals that prey on detritivores), specializing on entomobryomorph Collembola (Kennedy and Schramm 1933, Wilson 1950, Weber 1952, Wilson 1953, Brown and Wilson 1959, Masuko 1984, Dejean 1985, Deyrup and Cover 2009, Masuko 2009, Masuko 2009, Ohkawara, Nakamura et al. 2017) (and personal observations). In the southeastern United States, *Strumigenys* are the most diverse and often the most abundant ant in mesic forests. Because 45 species of *Strumigenys* found in the U.S. occur in the southeast, I chose to investigate local communities within the southeastern U.S. where species are most abundant and diverse.

4.3 METHODS

4.3.1 Statistical Methods

To test the four community assembly hypotheses (competition, phylogenetic conservation, evolutionary adaptation, and habitat filtering), I used *Niche* modeling software (Ulrich, Piwczynski et al. 2012). The data required by *Niche* consist of three input matrices, a species-by-site occurrence matrix, a site-by-environmental variables matrix (e.g., climate variables, vegetation categories), and a species-by-species phylogenetic or trait distance matrix. *Niche* then creates randomized occurrence matrices that represent null patterns against which the observed matrices are compared. This model records species co-occurrences in sites and uses the presence,

absence, and abundance of species in sites to statistically infer whether patterns of site-occupancy correlate with environmental variables at those sites and/or with the phylogenetic distance of species at those sites. Thus, the *Niche* model compares observed patterns to null expectations generated by randomizations of observed patterns. The analysis generates several submatrices for each pair of species to test for pair-wise spatial patterning in all two-site combinations. Submatrix *Together* describes a given pair of species occurring in the same site out of two sites [[1,0][1,0]]. Submatrix *Clumping* describes one pair of species occurring together in both of the pair of sites [[1,1][1,1]]. Submatrix *Checkered* describes one pair of species occuring in two sites, but not in the same two sites [[1,0][0,1]]. The model then extracts all of the Together, Clumping, or Checkered submatrices from the observed site-by-species matrix and computes the differences between the phylogenetic distance or difference between environmental variables over the pairs of species and pairs of sites. These values are then compared to values generated by randomized submatrix patterns. For example, to test for phylogenetic structure or environmental associations, for each pair of species, the model compares the observed phylogenetic(Δphyl) and environmental(Δenv) distances to the expected (Δphyl)/(Δenv) distance calculated from a randomized site-by-species matrix. Statistical significance is calculated by bootstrap from 1000 randomized matrices, accepting significance at the two-sided 5% error level. The model calculates standard effect sizes as *Z*-transformed scores by subtracting expected from observed values and dividing the difference by the standard deviation of expected value. The Ulrich *Niche* model tests for phylogenetic niche conservation and evolutionary adaptation using the Pearson coefficient of correlation between all Δenv and Δphyl for each metric (Together, Clumping, or Checkered). **Tables 4.3-6** lists *Z*-scores and *p* -values of each test (see **Figure 4.6** for interpreting *Niche* model results).

The hypothesis of phylogenetic niche conservation (ΔenvΔphyl) is supported when more closely related species pairs occupy more similar environments and/or more distantly related species occupy more dissimilar sites. The hypothesis of evolutionary adaptation (ΔenvΔphyl) is supported when more closely related species pairs occupy more dissimilar environments. Predictions of the competition hypothesis and evolutionary adaptation overlap. Lineages may diversify and expand into new environments, creating a phylogenetically differentiated pattern of allopatry not caused by past by competitive interactions. Only at smaller spatial scales of microsites and $25m^2$ local communities is the competition hypothesis distinguished from evolutionary adaptation. The competition hypothesis is supported by *Niche* metrics of phylogenetic dispersion (Δphyl) but only if micro allopatry is observed at the smallest spatial scale of microsites in which competitive interactions are possible. The Δphyl metric only describes species phylogenetic dispersion (not environmental differences) for pairs of species relative to the sites they inhabit. However, since species occupying the same sites experience more similar environments, Δphyl provides support to phylogenetic niche conservation, adaptive radiation, or competition, depending on spatial scale. Competition is supported if co-occurring species are more distantly related than expected at random in microsites (phylogenetically over-dispersed) and if more closely related species do not co-occur. If co-occurring species are phylogenetically over-dispersed in microsites, then competition probably affects microsite community assembly. In this case, the competition hypothesis can be also tested against in patterns of co-occurrence in local 25^2 communities at the next larger spatial scale. Additional support to the competition hypothesis would be if co-occurring species at small spatial scales are more phylogenetically niche differentiated according to *Niche* ΔenvΔphyl correlations. The hypothesis of habitat filtering (Δenv) is simply supported when species pairs tend to co-occur in

sites within a narrower range of environments than expected by the null model distribution of environmental variation.

I ran one of two null models in *Niche* depending on the collection method and species occurrence data in sites at each geographic scale. The first model assumed that the numbers of collections of a species in a given spatial unit reflected actual species abundances (abundances represent colonies and not individual ants) in that spatial unit (termed the ***rc*** model in *Niche*). The ***rc*** model compared observed species abundances to fixed row and column null matrices that kept total species abundances and abundances of species at sites equal to observed values. The second model (***s*-**null in *Niche*) used species presence-absence data and not abundance data. The fixed ***s*-**null model keeps site and species occurrence totals constant and at observed alues in null matrices. The ***s*-**null model does not assume collection records reflect species abundances. I ran the *Niche* ***s***-null model for 0.20 ha sites and microsites. Local 0.20 ha site samples are likely to over-represent species abundances due to collections of multiple specimens of the same species from the same colony. Local 0.10m^2 microsites are also more likely to overestimate species abundances for the same reason. I ran the ***rc*-**null model for bioregions and local 25 m^2 communtities. I chose bioregions based on areas with large collection records and rarified collection records by removing duplicate records of geographic occurrences to eliminate the problem of inflating abundances due to multiple specimen collections. Removing duplicate records removed repeated collections of the same space and separated collection locations by at least 1.1 meters. Collections in local communities in 5x5 m^2 areas better represent colony abundances over that spatial scale. This is because each occurrence within a microsite was at least 0.8 meters away from the next microsite (a large distance for a *Strumigenys* colony to occupy). With this distance between sampled microsites, then it is reasonable to assume that

abundances can be estimated by adding up species occurrences over all microsites (for a maximum of 25 occurrences) within a local 25m^2 area. Thus, each occurrence is therefore likely to be a different colony.

There are potential issues with using collection records to estimate species presence and abundance. This is because measuring collection effort by the number collection records in each bioregion is biased, namely that collection records do not correlate with collection effort. Collection records only produce data on species presence, and rarely on species absence. Species not collected in a geographic area may be truely absent in the area or may actually be present (false negatives). Areas with few species collection records may be either under-sampled or actually species-poor (or species there may have low abundances). Bioregions are a case in point that do not represent equal collection efforts. In this study, bioregions represent collection records obtained from the published literature, from museum specimens, and from online databases, and the number of collection records varies considerably among bioregions. West of the Mississippi River, collection records of *Strumigenys* drop sharply. This drop is probably due mainly to the actual rarity of *Strumigenys* in the western U.S. For example, New Mexico is one of the most intensely surveyed U.S. states for ants, and it has more recorded ant species than any other U.S. state (antweb.org). However, *Strumigenys* are relatively rare in New Mexico collections, and there are only three native species in the state. Similarly, many states have no *Strumigenys* collections, yet have been intensively surveyed for ants (Wheeler 1917, Creighton 1950, Gregg 1963, Wheeler and Wheeler 1986, Talbot 2012). California and New Mexico are the two western states with a known ant fauna that is more diverse than in any state east of the Mississippi River (antweb.org). *Strumigenys* species occurring in the western half of the U.S.

tend to be endemic species with small known ranges (species of the Nearctic clade), or to be species of different biogeographic origins that were probably introduced by humans.

As species abundances at sites are estimated from collection records, low collection numbers might underrepresent true abundances and the number of species present. For this reason, I ran three ***rc-***null models for bioregion collections, sucessively increasing the minimum number of collection records necessary for a bioregion to enter the analysis. These models made it possible to investigate the extent to which areas with few collection records influence model results. I provide more detail in the bioregion methods section below. Since all other collection records represent identical collection protocols and therefore equal collection effort for smaller spatial scales (0.02 ha areas, local $25m^2$ communities, and microsites), I assumed species collected at a site represented abundant species at those sites. False negatives may still present a problem in all models, and be most problematic when modelling species presence and absence. This is especially ture if rare species are rare everywhere and thus are likely to be absent due to undercollection. This is most problematic in 0.20 ha sites and bioregions. In 0.20 ha sites, species presence is estimated by subsamples of larger areas. The *Niche* model uses average euclidean distances between species pairs using either phylogenetic distance or the difference between environmental variables in sites where a species pair is compared. Therefore numbers of occurrences of rare species (either being present or absent) have less influence on *Niche* results (rare species are not weighted in the *Niche* model and therefore influence expected randomizations less than common species). The site-by-environmental variables and site-by-species matrices for each bioregion are described in the following subsections of Methods of data collection for each geographic scale.

For the *Niche* model, I used the phylobase package in *R* (R-Core-Team 2017) to construct an ultrametric tree that included only one specimen per species using our previously RAD-seq generated phylogeny (Chapter 3). An ultrametric tree is a phylogenetic tree that assumes the rate of genetic change is equal through time and equivalent among species. Ultrametric distance replaces triangle inequality distances between any pair of species arising from a terminal node and is calculated as the maximum distance between that terminal root node and each leaf (species tip). Distances between two terminal nodes species will be the same to any other species on the tree and is calculated by the additive length of distances of each node between species. I used ultrametric phylogenetic distances between any two species on the ultrametric tree to construct a species-by-species phylogenetic relatedness matrix using Euclidean distances of all U.S. species pairs occurring in each site within each geographic scale (bioregions, 0.20 ha communities, local communities, and microsites). For two species, *S. rogeri* and *S. emmae,* I used ultrametric values of their closest known relative that I sequenced based on morphological similarity and a previously reported phylogeny (Bolton 2000b, Ward, Brady et al. 2015). I produced two species-by-species phylogenetic matrices, one of all *Strumigenys* occurring in the U.S. and another of only species originating in the Nearctic. Species originating in the Nearctic form a closely related clade sharing phylogeographic evolutionary histories. Therefore, the assumption is that these species have had a greater potential to interact with each other. Recently introduced or migrant species may currently interact, but did not historically have the same potential to interact with each other because they have geographically separate origins (**Figures 4.1 & 4.2; Table 4.1**).

To assess environments at multiple geographic scales (bioregions and local communities of 0.20 ha and 25m^2 scales), I chose two climate variables for which data are available on multiple

spatial scales: mean annual temperature (MAT) and precipitation in driest quarter (PDQ) (see Chapter 3 for methods and rationale for choosing these two environmental variables). I did not use MAT and PDQ variables to define microsite environments because they are measured at a larger geographic scale and did not vary between microsites within the same local community. All other environmental variables of 0.20 ha communities, local communities, and microsites were the result of field measurements and described in the sections on geographical sample areas below.

The results of Chapter 2 showed that the distribution of species richness in randomly sampled 0.20 ha communities was bimodal, having more sites with more species and more sites with fewer species than expected binomial expectations. This result suggests that sites divide into similarly preferred or non-preferred areas across many species of *Strumigenys*, a finding that supports the hypothesis of habitat filtering. I tested whether species richness patterns support the habitat filtering hypothesis at larger spatial scales (bioregions), and I tested both the habitat filtering hypothesis and the competition hypothesis at smaller spatial scales (microsites). At smaller spatial scales, if species competitively exclude one another, fewer species would tend to co-occur than expected based on binomial expectations. These tests complement the *Niche* model since *Niche* does not evaluate general distributions of co-occurrences. I tested distributions of co-occurrence in sites (bioregions and microsites) to expectations of a random discrete Poisson distribution using JMP® statistical software (JMP® 1989-20016). I did not test 0.20 ha communities or local communities because I chose them non-randomly using the results of Chapter 2 to identify areas where *Strumigenys* were more likely to occur. Bioregions incorporated all known *Strumigenys* collected in the U.S. Microsite collections were evenly

sampled, equal-effort collections and included the entire area of a microsite within local communities.

To assess whether variation in 0.20 ha *Strumigenys* ant communities correlated variation in the types of vegetation, I compared similarities of tree species present in 0.20 ha communities to similarities of *Strumigenys* present in 0.20 ha communities. Using a Mantel statistical test, I compared similarities of species occurrences between tree species and *Strumigenys* species, tree species and geographic distance, and *Strumigenys* species and geographic distance between sites using the vegan package in the *R* statistical program (R-Core-Team 2017). I ran 10,000 permutations to generate null expectations for the Mantel bootstrap. Communities in 0.20 ha sites (0.20 ha sites) had the most complete information on tree communities (mean tree species per site = 4.2±2.6), the largest numbers of observations in 0.20 ha communities (n=280), and covered the largest geographic space in observed 0.20 ha communities (mean = 308.5 km between each 0.20 ha community with a range of < 1km to 724 km apart). I ran this test only for one geographic scale (0.20 ha communities) and both phylogenetic distance levels, for all U.S. *Strumigenys* species (henceforth, all U.S. species) collected in 0.20 ha community samples and for the Nearctic clade of *Strumigenys* species (Nearctic clade species). Smaller geographic scales were too small to assess tree communities.

4.3.2 Data Collection – Bioregional assemblages

To produce a site-by-species matrix for the *Niche* model for bioregions, I used the twenty-eight 60,000 km^2 bioregions with non-duplicate collection records of species in those bioregions to represent species presences and abundances (see Chapter 3 methods for data collection and additional justification; **Figures 4.1 & 4.3**). I assumed non-duplicate collection records represented abundance of ant colonies and not individual ants.

I ran three models to determine the influence of bioregions with few collection records on *Niche* model results. The first model (Model 1) assumed all areas had equal collection effort and collection records accurately estimated *Strumigenys* abundance and rarity. The minimum number of collection records for an area to be included in the first model was thirteen for all U.S. species, and one record for species of the Nearctic clade. The second model (Model 2) assumed collection efforts were small in any bioregion containing less than 55 specimen records for all U.S. species and containing less than 40 specimen records for Nearctic clade species. Model 2 also assumed regions with relatively low and low numbers just above the lower limit of collection records accurately reflected species abundances. I chose these lower limits purposefully because not including bioregions below these limits removed the most problematic undercollected regions that were in the southeastern U.S. next to bioregions with large numbers of collection records. The lower limit of collection records of Model 2 also did not eliminate most of the regions where intensive faunistic surveys nevertheless resulted in few *Strumigenys* collection records, probably because *Strumigenys* were truly rare in those regions. The third model (Model 3) assumed all bioregions with few collection records accurately estimated bioregions as having low *Strumigenys* abundances. The minimum number of collection records for an area to be included in the Model 3 was one hundred for all U.S. species and one hundred for Nearctic clade species. Model 1 results are influenced by rare western species occupying different climates (PDQ) and a higher likelihood of including false negatives in under-collected bioregions. Model 2 included most western bioregions and most northern peripheral bioregions, but excluded the most problematic undercollected bioregions located centrally in the southeastern U.S. This Model 2 should be influenced less by false negatives and more by western and peripheral bioregions. Model 3 excludes most western and bioregions on the

periphery of most U.S. species ranges. This model will be least influenced by false negatives and most influenced by the absence of peripheral and western bioregions. Bioregions in Model 3 are centered in the southeast and have smaller MAT and PDQ climatic ranges and are less phylogenetically inclusive. The results of this model are less influenced by climatic extremes and are more suitable for interpreting how species are distributed among environments.

To produce the environmental variables-by-site matrix needed for the *Niche* model of bioregions, I used two climate variables, mean annual temperature (MAT) and precipitation in driest quarter (PDQ). I obtained data on these climate variables using the dismo package in *R* (R-Core-Team 2017) to download data from BioClim.org Version 2.0 (Fick and Hijmans 2017) for each specimen collection record for each species in each 60,000 km^2. ANOVAs and *t*-tests between all bioregion pairs showed that variation within region is small and that mean MAT and PDQ were good estimates of the climate for each region. ANOVAs also revealed that species belonging to tropical clades often occurred in warmer and drier locations than did species belonging to the Nearctic clade collected within the same 60,000km^2 region. For this reason, I constructed mean value estimates of environmental variables for each region at each of the two phylogenetic levels (all U.S. species and Nearctic clade species phylogenetic distance levels).

4.3.3 Data Collection - Communities in 0.20 ha sites

From July 20 to October 25, 2013, I collected leaf litter samples in two hundred and eighty 0.20 ha sites in the southeastern U.S. (**4. 4**). I chose sites to represent natural habitat types that were located in protected areas and/or areas managed for habitat conservation. I laid out a square with an area of 0.20 in each site (**Table 4.7)**. I took GPS locations for each site using a Garmin® etrex Summit HC GPS. I obtained altitudes from GPS coordinates with Google Earth®. I sampled sites representing five types of vegetation: hardwood forest, pine forest, mixed pine and

hardwood forest, field without trees, and woodland with scattered trees. I quantified the vegetation by counting and identifying the tree species in each 0.20 ha community. I measured ground cover in a 15 cm diameter circle at the center of each meter along a 25 meter transect through the center of the 0.20 ha site. I classified habitats into four categories: bottomland (riverine floodplains), field (lacking canopies of trees in more than 50% of the site), woodland (having between 50-75% canopy cover), and forest (having touching canopied trees over 75% or more of the site). I took black and white panoramic pictures of each site, manually adjusted thresholds of each picture and calculated shade as the number of black pixels (trees and leaves) times 100 divided by the sum of white (sky) and black pixels using imageJ software (Schneider, Rasband et al. 2012). Shade provided a continuous numerical environmental variable for the *Niche* model. Shade significantly correlated with habitat categories and confirmed categorical placement of habitats. Fields had significantly lower shade cover than woodlands and woodlands had significantly lower shade values when compared to bottomlands or forests. Forests and bottomlands did not differ in shade values. I classified ground cover into one of five categories (bare ground (exposed soil), leaf litter, stone or rocks, herbaceous vegetation, or water) based on which category represented the majority of a sample site. At each meter along the transect, I also measured soil moisture, soil pH, and depth of leaf litter and recorded the means over the transect across the site (**Table 4.7**).

I used field methods that I had previously designed and optimized to sample and extract *Strumigenys* from leaf litter (**Chapter 2**). Within site I extracted sifted litter, woody debris, and organic soil from areas including, but not limited to: litter under open and closed canopy; around and under objects such as rocks, standing dead trees, and fallen logs and branches; and litter and soil from topographically distinct areas such as depressions, flat areas and slopes. I consolidated

samples until each sifted litter sample consisted of 3.75 l of sifted litter and organic debris. I resampled each site a second time following the exact protocol of the first sample, but I avoided sampling from the previous set of exact locations. I sampled between two and six sites per day on the first and repeat sampling, but I only collected environmental categorical habitat data on the first sample. I extracted ants and other litter arthropods using eight-quart Berlese funnels equipped with 40-watt bulbs above each litter sample. I placed the litter sample onto one-cm^2 wire mesh and collected the arthropods into labeled vials containing 95% ethanol. I ran the Berlese funnel extractions for twenty-four hours. I sorted wet samples under a Leica MZ8 microscope, identifying and counting all *Strumigenys* and point mounting representative individuals of each *Strumigenys* species in each sample. I deposited the specimens with the University of Georgia Natural History Museum's Collection of Arthropods. For *Niche* model runs I created a site-by-species matrix from occurrences of each species in each 0.20 ha community and a site-by-environment matrix from environmental measures (**Table 4.7 & 4.8**).

4.3.4 Data Collection – Local 25m^2 Communities and 0.10m^2 Microsites

From August 11, 2014 to October 19, 2014, I re-sampled twenty-three of the most diverse 0.20 ha communities (**Figure 4.5**). In each 0.20 ha community, I sampled two 5x5 m local communities. In each local community, I sampled the total leaf litter and organic debris in the central 0.10 m^2 area of each square meter. I defined each of these 0.10 m^2 areas as microsites. I collected all samples from a microsite in a single day. I followed the same protocol for collection and extractions of leaf litter as 0.20 areas except I used smaller standard Bioquip® Berlese funnels to extract arthropods from litter and used a 25-watt bulb for six hours.

I recorded the central GPS location of each local community within their respective 0.20 ha community. To quantify vegetation in each local community I identified and recorded all of

the tree species within five meters of the local community site. I also recorded their location in relation to the local community and the diameter at breast height (DBH) of each tree. In each microsite, I took four measurements of litter depth (mm) and organic humus layer (mm) and recorded their mean (mLit) and variance (vLit). I counted "small" sticks (< 10 cm in diameter, StickS), and "large" sticks (>10 cm and < 80 cm in diameter, StickL). I took soil moisture and soil pH measurements using a Kelway® soil tester in the center of each microsite. The soil tester is a conical metal object and depending on the ease of inserting it into the ground I categorized the soil as either compact, or loose. To observe the soil profile, I dug a hole 10 cm in diameter and 20 cm deep. I recorded the following soil characteristics: clay content, rocks (>10 cm in diameter), presence of a root mat, and sand content. I recorded data as presence or absence. I used total numbers of soil profiles in each characteristic category in 25 microsites of a local community to calculate average soil properties of local communities. In each square meter of a local community I measured the coverage of the following ground cover categories; branch (> 80 cm and < 120 cm in diameter), log (> 120 cm and lying vertical), stump (standing dead tree base), tree base (Tbase; base of live tree), depression (Dep.; having a marked depressed area within the square meter), and open (having no differing topological or biological structure). I created a site-by-species matrix from occurrences of each species in each local $25m^2$ community and $0.10m^2$ microsite and a site-by-environment matrix for each spatial scale from environmental measures (**Tables 4.9 & 4.10**).

To assess food availability for *Strumigenys* in microsites I counted the number of Entomobryomorph Collembola extracted from a subset of microsite samples (n = 126 of 1150 total) and performed a linear regression in JMP® between the number of Collembola extracted and the number of *Strumigenys* extracted.

4.4 RESULTS

4.4.1 Summary of Niche Model results

At the largest spatial scale of bioregions, presence-absence patterns and phylogenetic relatedness of all species supported phylogenetic niche conservation. The all species analysis included species of different lineages that evolved in diverse geographic areas and environments. Species within lineages are by definition more closely related and such within-lineage species tended to occur in the same sites. Within the climatic ranges that Nearctic species inhabited, species occurring in the same bioregions and pairs of species occurring in the same pairs of bioregions were more phylogenetically distant than expected according to the null *Niche* model and supported the Adaptive Radiation hypothesis (**Figures 4.7-8** and **Tables 4.3-6,** See **Figure 4.6** to interpret Figures).

At smaller spatial scales, Nearctic and all species exhibited identical presence-absence and phylogenetic relatedness patterns. These patterns support the same community assembly hypothesis on a given spatial scale. However, which hypothesis was supported depended on spatial scale. In 0.20 ha sites, communities contained more distantly related species than expected, supporting either the adaptive radiation hypothesis or the competition hypothesis. At smaller scales, $25m^2$ local communities and one-m^2 microsites, however, one can reject the competition hypothesis. Because the smaller scales do not support the competition hypothesis, the scales on which it is most likely to apply, I therefore also reject the competition hypothesis at the 0.2 ha scale as well. In $25m^2$ local communities, co-occurring species were more closely related than expected, which supports the phylogenetic niche conservation hypothesis. At the one-m^2 spatial scale, patterns of species relatedness could not be distinguished from random by

Niche null model comparisons and supported no assembly hypothesis. Additionally, in microsites there were no statistically significant correlations between presence-absence patterns and Δphyl, Δenv, or ΔphylΔenv (**Figures 4.7 & 4.9** and **Tables 4.3-6,** See **Figure 4.6** to interpret Figures).

The hypotheses of phylogenetic niche conservation, adaptive radiation, and habitat filtering hypotheses each gained support from expected presences-absence patterns over the three largest scales, but support of these hypotheses differed depending on the focal environmental variable and the phylogenetic level (Nearctic clade species or all species). These hypotheses are evaluated by each environmental variable over each spatial scale (**Figures 4.7 & 4.10** and **Tables 4.3-6,** See **Figure 4.6** to interpret Figures).

4.4.2 Mantel tests support habitat filtering

Mantel tests of community differences supported the hypothesis of habitat filtering of *Strumigenys* by tree communities at the 0.20 ha spatial scale. More similar tree communities have more similar *Strumigenys* communities of both Nearctic clade species and all species (**Table 4.2**). *Strumigenys* communities are also more similar in closer sites (R^2=0.17, $p < 0.001$), but the correlation with distance is much weaker than that of *Strumigenys* with tree communities (R^2=0.40, $p < 0.001$).

4.4.3 Tests of co-occurrence distributions

Bioregions tended to have either more or fewer species than expected by a Poisson distribution, suggesting *Strumigenys* have similar climate requirements in bioregions they inhabit and similar reasons from being absent from bioregions they do not inhabit (**Figure 4.11**). The fit of a Poisson

distribution of observed co-occurring species over microsites is strong, and the hypothesis of random species co-occurrence cannot be rejected (**Figure 4.12**).

4.4.4 Tests of Collembola in Microsites

Linear regression analysis of *Strumigenys* abundance by Entomobryomorph Collembola shows no relationship between Collembola abundance and *Strumigenys* abundance at the microsite scale ($R^2 < 0.001$, $F = 0.09$, $p = 0.76$, $n = 126$; **Figure 4.13**). Collembola occurred in every sample examined while *Strumigenys* only occurred in 46% of all microsites.

4.4.5 Niche model results of bioregions

Results of the *Niche* model proved robust to changes in presence-absence data of *Strumigenys* in U.S. bioregions under three models differing in minimum permitted number of collection records. Varying the cutoff for number of collection records did not greatly change major results or interpretations of the *Niche* model for bioregions (**Figures 4.7-8 & 4.14**, **Table 4.3**). Significant changes in results that supported competing hypotheses occurred only between Models 1 and 3 for the metric of Togetherness (for MAT) in the Nearctic clade species. Results of Models 2 and 3 became less or more strongly correlated by *Niche* metrics to environmental variables, but did not support competing hypotheses (discussed in detail below; **Figure 4.14**, **Table 4.3**).

4.4.5.1 Testing the Habitat Filtering Hypothesis (Δenv)

Species were strongly under- or over-dispersed with regard to their distributions under MAT and PDQ, but interpretations of habitat filtering were inconclusive at the spatial scale of bioregions. All U.S. species and Nearctic clade species showed similar affiliations to PDQ and different

affiliations to MAT by co-occurrence metrics (Clumping and Togetherness). PDQ was more dissimilar than expected between pairs of sites containing the same pairs of co-occurring species, a pattern not supporting the habitat filtering hypothesis. Contrasting this result, PDQ was more similar in sites where a pair of species co-occurred were more similar than sites they were both absent, a pattern consistent with habitat filtering. Co-occurrence among all U.S. species (Clumping) revealed that species tend to occupy a wider range of MAT bioregions than expected, whereas Nearctic clade species tended to be underdispersed when considering MAT. All U.S. species and Nearctic clade species that do not co-occur but occupy different sites (Checkered) tended to occupy more disimilar MAT sites. However, in the case of the Checkered metric of PDQ, all U.S. species tended to occupy more dissimilar PDQ sites whereas Nearctic clade species occupied more similar sites **Figure 4.8**, **Table 4.3**.

4.4.2.2 Testing the Phylogenetic Niche Conservation or Adaptive Radiation Hypothesis (Δphyl)

Strumigenys are phylogenetically under-dispersed in all three models for co-occurrence metrics (Togetherness and Clumping) in all U.S. species, supporting the phylogenetic niche conservation hypothesis. In Model 2 and Model 3, all U.S. species that occurred in separate sites were more closely related than expected (Checkered metric). For species of the Nearctic clade, co-occurring species were phylogenetically over-dispersed for Models 1 and 2 as well as over-dispersed by one of two metrics of co-occurrence for Model 3, a pattern consistent with the adaptive radiation hypothesis. Results of phylogenetic dispersion in all models had similar sign and *Z*-scores for phylogenetic structure for both all U.S. species and Nearctic clade species, but differed in significance (**Figure 4.7**, **Table 4.3**).

4.4.5.3 Testing the Phylogenetic Niche Conservation and Adaptive Radiation Hypotheses to Specific Environmental Variables (RΔenvΔphyl)

Correlations of phylogenetic relationship with MAT of sites where species occurred were similar for most models of all U.S. species and Nearctic clade species. However, correlations with PDQ of phylogenetic relatedness of sites-by-species occurrences varied in all U.S. species (by model), but not Nearctic clade species. In all U.S. species, more closely related species tended to co-occur in more similar MAT sites, whereas species co-occurring in more dissimilar MAT sites were more distantly related, a pattern supporting phylogenetic niche conservation (Clumping metric, all models). All U.S. species had a different pattern supported by all models, namely that co-occurring species that were more distantly related occupied more similar MAT sites (a pattern consistent with phylogenetic niche conservation). All U.S. species that occurred in different sites were more distantly related and tended to occupy more similar MAT sites, this pattern is not inconsistent with phylogenetic niche conservation, but does not support any hypothesis (see discussion). For all U.S. species, PDQ weakly explains phylogenetic differences between species presence-absence and RΔenvΔphyl of PDG gave inconsistent results. Model one togetherness metrics of PDQ supports the conclusion that species pairs occurring in the same pair of sites and avoiding a different pair of sites are more closely related in sites they occupy, but PDQ of sites they occupy do not differ more than expected PDQ. In Model 2, the model suggests results are random. The results of Model 3 are not significant.

Correlations between PDQ and phylogeny are significant in all models by the Clumping metric for Nearctic clade species. Pairs of species of the Nearctic clade were more closely related and co-occurred in pairs of sites with more similar PDQ, supporting the phylogenetic niche conservation hypothesis. These results were not affected by omission of western species

excluded in Models 2 and 3, as Models 2 and 3 had larger standard effect sizes *Z*-scores. Pairs of Nearctic clade species that co-occurred and were absent from the same pair of sites were more closely related (Togetherness), yet these same pairs of sites had a wider range of PDQ than expected (significant and similar for Models 1 and 2; **Figure 4.8**, **Table 4.3**).

4.4.6 Niche model results of 0.20 ha communities

4.4.6.1 Testing the Habitat Filtering Hypothesis (Δenv)

At the 0.20 ha community scale, Z-scores of *Niche* model results for species associated by environmental variables had low standard effect sizes. No environmental variable supported the habitat filtering hypothesis with all three *Niche* metrics (Clumping, Togetherness, and Checkered) for either the Nearctic clade species or all species (**Figure 4.9**, **Table 4.4**).

4.4.6.2 Testing the Phylogenetic Niche Conservation or Adaptive Radiation Hypothesis (Δphyl)

Both all U.S. species and Nearctic clade species are more distantly related in 0.20 ha sites where they co-occur. All U.S. species are phylogenetically over-dispersed by all metrics and Nearctic clade species are phylogenetically over-dispersed for two of three metrics (Togetherness and Checkered). Clumping correlations are not significant. This suggests more distantly related species tend to co-occur in the same 0.20 ha site and more closely related species occupy different sites when they do not co-occur, all patterns together strongly support the adaptive radiation hypothesis at the 0.20 ha spatial scale (**Figure 4.7**, **Table 4.4**.).

4.4.6.3 Testing the Phylogenetic Niche Conservation and Adaptive Radiation Hypotheses to Specific Environmental Variables (RΔenvΔphyl)

All species show RΔenvΔphyl patterns consistent with the niche conservation hypothesis by *Niche* co-occurrence metrics of Clumping and Togetherness for latitude, altitude, PDQ, and shade. Species pairs that don't co-occur in the same pair of sites (Checkered metric) also tend to be more phylogenetically different in more dissimilar MAT sites and more closely related in more similar MAT sites, also supporting phylogenetic niche conservation, whereas only two environmental variables (plant cover and stone cover) support the adaptive radiation hypothesis by the Checkered metric, having weak but significant standard effect sizes.

Significant correlations between environmental variables and phylogenetic relatedness in Nearctic species mostly supported the adaptive radiation hypotheses (five of seven significant correlations), but significant results were had small standard effect sizes with contrasting support for phylogenetic niche conservation by Togetherness for shade and support for adaptive radiation by Clumping for shade. The checkered metric of three environmental variables (latitude, altitude, and PDQ) supports the adaptive radiation hypothesis, as species that occur in different sites but not together are more closely related and occupy more dissimilar environments (**Figure 4.9**, **Table 4.4**).

4.4.7 Niche model results of 25m^2 Local Communities

4.4.7.1 Testing the Habitat Filtering Hypothesis (Δenv)

Patterns of presence-absence of all U.S. species supported habitat filtering by some environmental variables, environmental over-dispersion of species by others, and mixed support of habitat filtering or environmental over-dispersion by two. The habitat filtering hypothesis is

supported by at least one *Niche* metric for climatic environmental variables (altitude and PDQ) soil variables (soil moisture, clay soils, and variance of litter depth), habitat characteristics (similar sized forests - DBH, the percent of hardwoods in a community – HW) and the number and type of available nesting site (the number of branches, the number of logs, and the number of stumps). Metrics of co-occurring species (Clumping or Together) occupied sites with more dissimilar environments of MAT, sandy soils, number of small sticks, number of trees, and forests with less woody structure (ground cover termed open).

Patterns of presence-absence of Nearctic clade species strongly support habitat filtering, more species occurred more often in similar environments in 14 of 24 environmental variables and occurred in more dissimilar environments by only three variables. Nearctic clade species occurred in similar environments estimated by climatic variables (altitude and PDQ), soil variables (soil moisture, mean litter depth, variance of litter depth, loose soils, and rocky soils), habitat characteristics (the percent of hardwoods in a community), and the number and type of available nesting site (the number of branches, the number of logs, and the number of stumps). The three environmental variables Nearctic clade species were over-dispersed were the number of small sticks, the average tree size in their community, and the area of ground coverage classified as open (**Figure 4.10**, **Table 4.5**).

4.4.7.2 Testing the Phylogenetic Niche Conservation or Adaptive Radiation Hypothesis (Δphyl)

All species and Nearctic clade species were phylogenetically under-dispersed supporting phylogenetic niche conservation at the local 25m^2 spatial scale. Co-occurring species tended to be more closely related in all U.S. species and Nearctic clade species, and species occurring in

different sites tended to be more distantly related by the Checkered Δphyl metric for all U.S. species (**Figure 4.7**, **Table 4.5**).

4.4.7.3 Testing the Phylogenetic Niche Conservation and Adaptive Radiation Hypotheses to Specific Environmental Variables (RΔenvΔphyl)

All U.S. species were more phylogenetically closely related and occupied sites with more dissimilar environments by eight environmental variables supporting the adaptive radiation hypotheses of these variables (altitude, mean litter depth, litter depth variance, clay soils, sandy soils, number of tree bases, and number of depressions in a local 25^2 community). All species were more phylogenetically related and occupy sites with similar environments supporting phylogenetic niche conservation to two environmental measures (latitude and number of large sticks in a local community). Nearctic clade species were more closely phylogenetically related and occupy sites with similar environments supporting phylogenetic niche conservation for ten environmental variables (altitude, MAT, soil moisture, mean litter depth, number of large sticks, average tree size, sandy soils, number of tree bases, number of branches, and open ground). Correlations between phylogenetic relatedness and environmental dissimilarity among occurring species supported evolutionary adaptation to only five environmental variables (latitude, PDQ, loose soil, number of tree bases, and number of logs). All U.S. species and Nearctic clade species had contrasting RΔenvΔphyl between *Niche* metrics in latitude, altitude, mean litter depth, and number of tree bases.

All U.S. species did not have significant RΔenvΔphyl results for MAT and PDQ. Co-occurring Nearctic clade species were closely related in sites that were more similar in MAT and did not co-occur in sites that were more different in MAT. The correlations was opposite for Nearctic clade species with respect to PDQ, co-occurring species tended to be more closely related and

occupy sites that were more different in PDQ than in sites where they did not co-occur (**Figure 4.10**, **Table 4.5**).

4.4.8 Niche model results of Microsites

At the spatial scale of microsite, *Niche* metrics produced no significant relationships between species occurrences and environment (Δenv), phylogeny (Δphyl), or correlations between changes in phylogenetic relatedness and changes in environment (RΔenvΔphyl). *Niche* model results suggest relationships of species occurrences with respect to conspecific *Strumigenys* and their environment is no different from random expectation at this smallest spatial scale (**Table 4.6**). These results do not support any community assembly hypothesis at this scale.

4.5 DISCUSSION

In Bioregions, when comparing all *Strumigenys* in our analyses occurring in the U.S., the *Niche* null model results of phylogenetic niche conservation is driven by the average phylogenetic distances of species from the Nearctic clade. Species of the Nearctic clade are extremely closely related and occupy cooler, moister environments compared to other species present in the U.S. of more distantly related species of tropical or subtropical origins. The *Niche* model provides results congruent with average MAT and PDQ collection locations of the Nearctic clade species when compared to other biogeographic clades (**Chapter 3**). Though phylogenetic niche conservation of phylogenetic all U.S. species is supported, phylogenetic over-dispersion is revealed in the more closely related biogeographic clade of Nearctic clade species (at this geographic scale of bioregions). These results do not support phylogenetic niche conservation and suggest that more distantly related species evolved in and occupy different environments within bioregions. This

logic is supported by results of habitat filtering and phylogenetic under-dispersion at smaller geographic scales of local communities. Recent geological processes likely contributed to the geographic range mixing of species at the biogeographic level. Over the last 2.58 mya, there has been at least 17 glacial-interglacial periods (Rial 1999) and these changing environments promoted range and environmental shifts, adaptive selection and speciation, and influenced both geographic mixing and separation of species (Augustin, Barbante et al. 2004). Phylogenetic over-dispersion at the larger bioregional and regional community scale could be the result of species range mixing over recently shared geological histories.

Bioregions are large, and species of different biogeographic regions could occupy different environments within regional sites. The same can be said of 0.20 ha sites, which, although a lot smaller than the bioregions, are still enormous on the scales relevant to the ecology of individual *Strumigenys* colonies. To a two-mm long ant, 0.20 ha sites are huge areas and species occurring within these communities may or may not occupy similar microenvironments. Of two hundred eighty 0.20 ha communities sampled within an area the size of six bioregions, all *Strumigenys* species still tended to be phylogenetically over-dispersed, supporting phylogenetic niche conservation. However, at the 0.20 ha spatial scale, there is support for habitat filtering, which came from relatively strong correlations between tree communities and *Strumigenys* communities (R^2 = 0.4 for all species and Nearctic clade species). Habitat filtering and phylogenetic niche conservation may also explain the phylogenetic over-dispersion of species of the Nearctic clade in bioregions and 0.20 ha communities if distantly related species occurring in the same bioregion or 0.20 ha community are occupying different geographic and environmental space. Support for this interpretation comes from the fact that tropical species are collected in

different locations with higher mean annual temperatures within the same bioregion compared to species of the Nearctic clade (**Chapter 3)**.

At the finer geographic and environmental scales of $25m^2$ local communities, scattered over an area nearly equal to a single 60,000 km^2 bioregion, I investigated forty-six $25m^2$ local communities. Remarkably, half the *Strumigenys* species known to occur in the U.S. occurred in these 46 local communities, which, when combined, is an area seven billion times smaller than the continental US. Local $25m^2$ communities together contained only about 20% of the total range of environmental differences of MAT and PDQ compared to all bioregions (**Table 4.1***)*. For both Nearctic clade species and all species, the habitat filtering hypothesis was supported for PDQ and soil moisture, suggesting species prefer similarly moist sites at smaller spatial scales. *Niche* model results of *Strumigenys* occurrences in local communities strongly supported predictions of habitat filtering and phylogenetic niche conservation. This suggests that at the scales of bioregions and 0.20 ha communities, phylogenetic over-dispersion, supporting the adaptive radiation hypothesis, was principally due to distantly related species occupying different environments within the same bioregion or 0.20 ha community. At increasingly smaller spatial scales MAT and PDQ climate variables become more similar and less important to explaining phylogenetic niche conservation. In $25m^2$ local communities, phylogenetic niche conservation is explained more by micro-environmental variables such as soil properties (rocky soils, clay soils, soil moisture), and potential nesting sites (branches and logs). However, since the geographic area including all local communities is the size of a single bioregion, additional studies of local communities in other bioregions are necessary to determine the strength of these conclusions.

At the smallest geographic and environmental scale of microsites, the *Niche* model of *Strumigenys* distributions with respect to co-occurrences, phylogeny, and environments does not

support the competition hypothesis. At this small scale, the presence or absence of *Strumigenys* species could be largely driven by sampling artifacts, with a low probability of sampling any given species. This could weaken the power of tests to detect competitive effects. Whatever the case, co-occurrence patterns on the smallest spatial scale could not be distinguished from random. Despite a lack of clear results of competitive interactions in microsites, the results of phylogenetic over-dispersion at larger geographic scales support the inference that distantly related species occupy more dissimilar environments and perhaps speciated allopatrically within larger geographic areas. It was also interesting that *Strumigenys* abundance and the abundance of their food, Collembola, were completely uncorrelated at the scale of microsites. I do not expect this result to change with an increase in sample size because the effect size and correlation between *Strumigenys* and Collembola abundance are near zero. This result strongly suggests that *Strumigenys* are not food-limited and that *Strumigenys* do not limit Collembola abundance. However, across heterogeneous landscapes at larger scales, Collembola may not always be as abundant as found in local microsites within a small bioregion and could possibly limit distributions and abundances of *Strumigenys* in drier bioregions where *Strumigenys* are less common.

4.6 CONCLUSIONS

This study explored four hypotheses, phylogenetic niche conservation, evolutionary adaptation, habitat filtering, and competition to explain the distribution and co-occurrence of species in the ant genus *Strumigenys* on four very different spatial scales in North America, in relation to climate and other environmental variables. North American *Strumigenys* divide into a Nearctic clade of endemics and a miscellany of exotic species from other biogeographic regions. At the

largest geographic scale, of 60,000km^2 bioregions, species of the Nearctic clade occupy more similar climates compared to the exotic, more distantly related species. This pattern supports the hypotheses of phylogenetic niche conservation and habitat filtering of lineages of *Strumigenys*. However, species within the Nearctic clade (lineage) were phylogenetically over-dispersed but occupied more similar environments, supporting both habitat filtering and the adaptive radiation hypothesis. At the next smaller geographic scale of 0.20 ha, all North American species were again phylogenetically over-dispersed, while more closely related Nearctic endemics tended to occur in more similar environments, supporting phylogenetic niche conservation and habitat filtering. There was additional support of habitat filtering from the finding of co-variation between *Strumigenys* communities and tree communities. At an even smaller geographic scale of species occurring in 25m^2 local communities, co-occurring species are phylogenetically under-dispersed and more closely related species tend to occupy more similar environments, once again strongly supporting phylogenetic conservation and habitat filtering. At the smallest geographic scale of species occurring in 0.10m^2 microsites, species tending to co-occur in sites are not phylogenetically different than expected at random. Species occurrences and co-occurrences in microsites are also not distinguishable from random and do not correlate to any measured environmental variables. There is no evidence that competition has influenced assemblage patterns of *Strumigenys* communities at any geographic scale.

4.7 List of Figures

Figure. 4.1. Overlaid ranges of all *Strumigenys* occurring in the US. Overlayed ranges of species of Nearctic (Blue), Neotropical (red), Australasian (yellow), and Afrotropical (green) species that migrated or were introduced here. The average phylogenetic relatedness among all species is 0.013 (0.001 min, 0.025 max). Geographical data are consistent with the hypothesis that more closely related species of biogeographic clade prefer similar environments to ones they evolved.

Figure. 4.2. Overlaid ranges of all *Strumigenys* of the Nearctic clade occurring in the US. Overlayed ranges of North American Strumigenys belonging to the Nearctic clade. These species likely evolved in the last 5-10 million years and are more closely related than any other biogeographic clade. The average phylogenetic relatedness among Neotropical species is 0.004 (0.001 min, 0.005 max).

Figure 4.3. Twenty-eight 60,000 km^2 bioregions. At the broadest scale, these bioregions contained the largest number of *Strumigenys* collection records and were large enough to capture gross changes in species assemblages and environmental differences across US *Strumigenys* ranges (see **Table 4.1**).

Figure 4.4. Two hundred and eighty 0.20 ha regional communities sampled in the southeastern US. At the regional scale, collections across the southeastern US occupy an area equal to about six bioregions. Climate ranges across all regional communities are much less than bioregions and contain 42% of MAT and 58% of PDQ ranges observed across all bioregions (see **Table 4.1**).

Figure 4.5. Twenty-three regional communities of the southeastern US each containing two local communities (25 m^2) made up of twenty-five microsites (one-m^2) each. At the local community scale, collections across the southeastern US occupy an area equal to about one bioregion. Environmental measures of climate (MAT and PDQ) of local communities contains about 20% of the range of values observed across all bioregions (see **Table 4.1**).

Figure 4.6. Interpreting *Niche* model results

Niche calculates the Euclidean differences or Pearson's coefficient of correlation between all the observed vs expected submatrices present in the species-sites matrix with respect to phylogeny or an environmental variable. The three metrics of submatrix patterns (two sites and two species per submatrix) are Togetherness (a pair of species occurs in the same site and are absent from the same site), Clumping, (a pair of species occurs in two sites), and Checkered (a pair of species occupy different sites; **Table 4.5**). The metrics $Clumping_{\Delta env}$, $Clumping_{\Delta phy}$, $Togetherness_{\Delta env}$, $Togetherness_{\Delta phy}$, and $Checkered_{\Delta env}$, $Checkered_{\Delta phy}$ are defined as the average Euclidean difference of all pairwise phylogenetic distances between species (Δphyl), and differences in an environmental variable (Δenv). RΔenvΔphyl is defined as the Pearson coefficient of the correlation between all the $Clumping_{\Delta env\Delta phy}$, $Togetherness_{\Delta env\Delta phy}$, and $Checkered_{\Delta env\Delta phyl}$ submatrices present in the species-sites matrix, and Δenv & Δphyl. $Clumping_{\Delta env\Delta phy}$ - A positive correlation between Δenv and Δphyl (RΔenvΔphyl) indicates joint occurrences of phylogenetically closely related species in similar habitats and joint occurrences of phylogenetically distant species in dissimilar habitats. If this joint occurrence of $Clumping_{\Delta env\Delta phy}$ is caused by similar ecological requirements, it would suggest the existence of niche conservatism. In contrast, a negative correlation between environmental differences among

sites and phylogenetic distances between species of $Clumping_{\Delta env \Delta phy}$ occurrence would show that phylogenetically distant species co-occur in ecologically similar habitats. For togetherness submatrices, positive $Togetherness_{\Delta env \Delta phy}$ correlations indicate that phylogenetically related species have identical patterns of occurrences in environmentally similar and dissimilar sites. Negative $Togetherness_{\Delta env \Delta phy}$ correlations indicate that phylogenetically related species have identical patterns of occurrences in environmentally dissimilar sites. For $Checker_{R\Delta env \Delta phyl}$ submatrices, a positive correlation between environmental and phylogenetic distances implies that phylogenetically distant species pairs are segregated across environmentally different sites. Phylogenetic over-dispersion (PO) reveals more distantly related species tend occur in the same sites more often than expected by *Niche* null models. At large scales Phylogenetic over-dispersion supports the adaptive radiation hypothesis, and in microsites phylogenetic dispersion supports the competition hypothesis. Phylogenetic under-dispersion (PU) supports the phylogenetic niche conservatism hypothesis. Niche (NC) reveals a positive correlation between closely related species occurring in sites with more similar environments and supports the phylogenetic niche conservatism hypothesis. Niche differentiation (ND) reveals closely related species occupy more dissimilar sites. At large scales ND supports the adaptive radiation hypothesis, and in microsites ND supports the competition hypothesis. Environmental under-dispersion (EU) supports the habitat filtering hypothesis, and environmental over-dispersion suggests species occupy a wider range of environments than expected.

Figure 4.7. *Niche* results of all spatial scales for tests of phylogenetic niche conservation vs. the adaptive radiation hypothesis. Summarized interpretaions of *Niche* model results of bioregions. In parentheses are interpretations of phylogenetic niche conservation (+) or adaptive radiation (-)

for p-value threshold of 0.05. See **Figure 4.6**. for additional interpretations and **Figures 4.14-16** and **Tables 4.3-5** for full model results and model parameters. Clumping = CL, Togetherness = TG, Checkered =CK) metrics.

Figure 4.8. *Niche* results of 60,000 km^2 bioregions. Summarized interpretaions of *Niche* model results of bioregions. In parentheses are interpretations of Z-scores for (Clumping = CL, Togetherness = TG, Checkered =CK) metrics HF refers to the habitat filtering hypothesis. A (+) supports the habitat filtering hypothesis and a **(-)** reports over-dispersion of *Strumigenys* to an environmental variable. PNC refers to the phylogenetic niche conservation hypothesis. A (+) supports phylogenetic niche conservation and a (-) supports the adaptive radiation hypothesis. In parentheses are each model run (model 1 / model 2 / model 3). See **Figure 4.6**. for additional interpretations and **Figures 4.14** and **Table 4.3** for full model results. All results reported have p-values < 0.001. Each * refers to the number of models with significant results. Model parameters, mean response *rc*-null model, iterations = 1000. Results in parentheses are of model 1-3 runs using Minimum Collection Records (MCR) of 13, 55, and 100 per region for all species, and MCR = 1, 40, and 100 for Nearctic clade species. All species model 1-3 parameters MCR = 13, n species = 42, n sites = 28, matrix fill = 0.343; MCR = 55, n species = 41, n sites = 21, matrix fill = 0.398; MCR = 100, n species = 37, n sites = 17, matrix fill = 0.493. Nearctic clade species model 1-3 parameters MCR = 1, n species = 30, sites = 27, matrix fill = 0.40; MCR = 40, n species = 29, n sites = 21, matrix fill = 0.452; MCR = 100, n species = 25, n sites = 17, matrix fill = 0.581.

Figure 4.9. *Niche* results of 0.20 ha communities. *Niche* model results of regional communities. In parentheses are interpretations of Z-scores for (Clumping = CL, Togetherness = TG, Checkered =CK) metrics. HF refers to the habitat filtering hypothesis. A (+) supports the habitat filtering hypothesis and a **(-)** reports over-dispersion of *Strumigenys* to an environmental variable. PNC refers to the phylogenetic niche conservation hypothesis. A (+) supports phylogenetic niche conservation and a (-) supports the adaptive radiation hypothesis. See **Figure 4.6.** for interpretations and **Figure 4.15** and **Table 4.4** for complete results. In bold are significant results of a p-value threshold of 0.05, * refers to a p-value threshold of 0.001, ** to a p-value threshold of 0.0001.

Figure 4.10. *Niche* results of local 25m^2 communities. *Niche* results of local communities. In parentheses are interpretations of Z-scores for (Clumping, Togetherness, Checkered) metrics (see **Figure 4.6.** for interpretations). In bold are significant results of a p-value threshold of 0.05, * refers to a p-value threshold of 0.01, ** to a p-value threshold of 0.001. Model Parameters, iterations = 1000, fixed weights *rc*-null model based on abundances of species in each site, EU=Environmental Under-dispersion, EO=Environmental Over-dispersion, PO=Phylogenetic Over-dispersion, PU=Phylogenetic Under-dispersion, ND=Phylogenetic (Niche) Differentiation, and NC=Phylogenetic (Niche) Conservatism (see **Table 4.5.** for numerical results of *Niche* model runs of local communities).

Figure 4.11. Poisson expectation fit of number of species occurring in bioregions. Level 2 Bioregions, Mean = 15.18±7.48, goodness of fit to Poisson distribution $X^2 = 382$, $p < 0.001$, $n =$

28 Bioregions tended to have fewer or more species than expected at random. Small p-values test the hypothesis that observed distribution does not fit a Poisson distribution and is accepted.

Figure 4.12. Poisson expectation fit of number of species occurring in microsites. Mean 0.58±0.73 *n*=1150 Goodness of fit to Poisson distribution X^2 1065, $p = 0.99$. Small *p*-values test the hypothesis that observed distribution does not fit a Poisson distribution and is rejected.

Figure 4.13. Numbers of *Strumigenys* extracted in microsite samples by the number of Entomobryomorph Collembola extracted from microsites. Collembola abundance does not predict *Strumigenys* abundance at microsites ($R^2 = < 0.001$, $F = 0.09$, $p = 0.76$, $n = 126$). Collembola occurred in every sample examined while *Strumigenys* only occurred in 46% of all microsites.

Figure 4.14. Detailed *Niche* results of Bioregion sites. *Niche* model results of bioregions. Top three rows of each Level are Z-scores for each model run in parentheses (model 1, model 2, model 3). Bottom three rows are interpreted results (see **Figure 4.6**. for interpretations). In bold are significant results, all results reported had p-values below 0.001. Each * refers to the number of models with significant results. Model parameters, mean response *rc*-null model, iterations = 1000. Results in parentheses are of model 1-3 runs using Minimum Collection Records (MCR) of 13, 55, and 100 per region for all species, and MCR = 1, 40, and 100 for Nearctic clade species. All species model 1-3 parameters MCR = 13, n species = 42, n sites = 28, matrix fill = 0.343; MCR = 55, n species = 41, n sites = 21, matrix fill = 0.398; MCR = 100, n species = 37, n sites = 17, matrix fill = 0.493. Nearctic clade species model 1-3 parameters MCR = 1, n species = 30, sites = 27, matrix fill = 0.40; MCR = 40, n species = 29, n sites = 21, matrix fill = 0.452;

MCR = 100, n species = 25, n sites = 17, matrix fill = 0.581 (see **Table 4.3.** for numerical results of *Niche* model runs of bioregions).

Figure 4.15. Detailed *Niche* model interpretations of 0.20 ha sites. *Niche* model results of regional communities. In parentheses are interpretations of Z-scores for (Clumping, Togetherness, Checkered) metrics (see **Figure 4.6.** for interpretations). In bold are significant results of a p-value threshold of 0.05, * refers to a p-value threshold of 0.001, ** to a p-value threshold of 0.0001. Model Parameters, iterations = 1000, mean response of fixed-fixed *s*-null model based on species occurrences at each site. Level 1, species = 29, sites = 223, occurrences = 585, matrix swaps = 81,200, matrix fill = 0.09. Level 2, species = 21, sites = 179, occurrences = 405, matrix swaps = 58,800, matrix fill = 0.108. EU=Environmental Under-dispersion, EO=Environmental Over-dispersion, PO=Phylogenetic Over-dispersion, PU=Phylogenetic Under-dispersion, ND=Phylogenetic (Niche) Differentiation, and NC=Phylogenetic (Niche) Conservatism (see **Table 4.4.** for numerical results of *Niche* model runs of regional communities).

Figure 4.16. Detailed *Niche* interpretations of local $25m^2$ communities. *Niche* results of local communities. In parentheses are interpretations of Z-scores for (Clumping, Togetherness, Checkered) metrics (see **Figure 4.6.** for interpretations). In bold are significant results of a p-value threshold of 0.05, * refers to a p-value threshold of 0.01, ** to a p-value threshold of 0.001. Model Parameters, iterations = 1000, fixed weights *rc*-null model based on abundances of species in each site, EU=Environmental Under-dispersion, EO=Environmental Over-dispersion, PO=Phylogenetic Over-dispersion, PU=Phylogenetic Under-dispersion, ND=Phylogenetic

(Niche) Differentiation, and NC=Phylogenetic (Niche) Conservatism (see **Table 4.5** for numerical results of *Niche* model runs of local communities).

4.8. List of Tables

Table 4.1. Scales of US *Strumigenys* geographic and climatic ranges examined.

Range Examined is the area of a polygon containing all sites, Site Size is the area sampled in each site, n=46 local communities, n=280 regional communities, n=28 bioregions, Nearctic Sp. is the total number of species of the Nearctic clade recovered in the all the samples of a particular geographic scale, Other Sp. is the total number of species not of the Nearctic clade recovered in the all the samples of a particular geographic scale, MAT is mean annual temperature in C°, PDQ is precipitation in driest quarter. Microsites, not tabled, are 0.10 m^2 and 25 microsites made up a single local community. I sampled two local communities in 23 regional communities. PDQ and MAT climate measures did not differ below the scale of local communities. All the local communities examined fit within a polygon area the size of a single bioregion and all regional communities examined fit within a polygon area the size of six bioregions. The geographic area encompassed decreases with the geographic scale examined an so do environmental ranges. At finer geographic scales, environmental differences between sites decreases. Results of species or phylogenetic structure associated to environments at finer geographic scales provides stronger support to habitat filtering and phylogenetic conservatism/differentiation than does associations of species over larger environmental (and geographic) distances.

Table 4.2. Table of results of Mantel tests between regional community geographic distances, tree species, and *Strumigenys* species. Correlational values are Pearson correlation coefficients.

Tree and *Strumigenys* species distance matrices were Euclidean distances of species being present or absent for each pair of regional community sites (n=280 regional communities). Tree and *Strumigenys* communities became more distant with increasing distance but the effect of geographic distance on community distance was much weaker than the correlation between *Strumigenys* species present in a regional community and tree species present (of either phylogenetic level).

Table 4.3. Table of full *Niche* model results for bioregion sites. Species Occ. = species occurrence, Phyl Dist = phylogenetic distance, EnvVar = environmental variance. See methods for descriptions of variables.

Table 4.4. Table of full *Niche* model results for 0.20 ha sites. Species Occ. = species occurrence, Phyl Dist = phylogenetic distance, EnvVar = environmental variance. See methods for descriptions of variables

Table 4.5. Table of full *Niche* model results for local $25m^2$ communities. Species Occ. = species occurrence, Phyl Dist = phylogenetic distance, EnvVar = environmental variance. See **Table 4.6** for site name definitions, and see methods for descriptions of variables.

Table 4.6. Table of full *Niche* model results for $0.10m^2$ Microsites. Species Occ. = species occurrence, Phyl Dist = phylogenetic distance, EnvVar = environmental variance. See **Table 4.6** for site name definitions, and see methods for descriptions of variables.

Table 4.7. Regional community observed environmental variables.

LAT=latitude, LON=longitude, ALT = altitude, Shade=insolation, LitterD=mean litter depth, % = ground cover percentage for B=bare ground, L=litter, P=Plant, S=Stone, W=water, MAT=mean annual temperature, PDQ=precipitation in driest quarter. APA=Apalachicola Forest, BER=Berry College, BKR=Black River Forest, BUR=Burke's Mountain, CRK=Crooked River State Park, FDR=Franklin Deleanor Roosevelt State Park, GCF=General Coffee State Park, GRB= Grand Bay Forest, HAN=Hannahatchee Wildlife Management Area , LWP= Laura Walker State Park, MDY=Moody Forest Conservation Area, MSP=Magnolia Springs State Park, MZA=Montezuma Conservation Area, OCA=Ocala State Fores, OCN=Oconee National Forest, OHP=Ohoopee Dunes Conservation Area, OKY= Ocmulgee Wildlife Management Area , PIN=Pinhoti Trail and Cumberland Plateau Forests, PRC=Providence Canyon State Park, RDH=Red Hills Preserve, SCN=Sandy Creek Nature Center, SMN=Seminole State Park, SPL=Splinter Hill Conservation Area, SRS=Savannah River Site, TAL=Tallulah Gorge, TTR=Tall Timbers Preserve, TUG=Tugaloo State Park, TWN=Townsend State Forest, WDT=Wade Tract Forest, WWF=White Water Falls, see methods for descriptions of variables.

Table 4.8. *Strumigenys* occurrence by 0.20 ha sites.

Table 4.9. Observed environmental variables of local communities. LAT=latitude, LON=longitude, ALT = altitude, MAT=mean annual temperature, PDQ=precipitation in driest quarter, SM=soil moisture, mLit=mean litter depth, vLit=variance of litter depth, SticksS=sticks < 10mm, SticksL = Sticks > 10mm, nTrees = number of trees, DBH=mean tree diameter at

breast height, HW=percent of hardwood trees verses conifers in the site, TreeS=number of tree species in the site, TreeDiv=Fishers' alpha, Dep.=Depression, See **Table 4.6** for site name definitions, and see methods for descriptions of variables.

Table 4.10. *Strumigenys* occurrences in microsites within local communities.

4.9. Figures and Tables

Figure. 4.1.

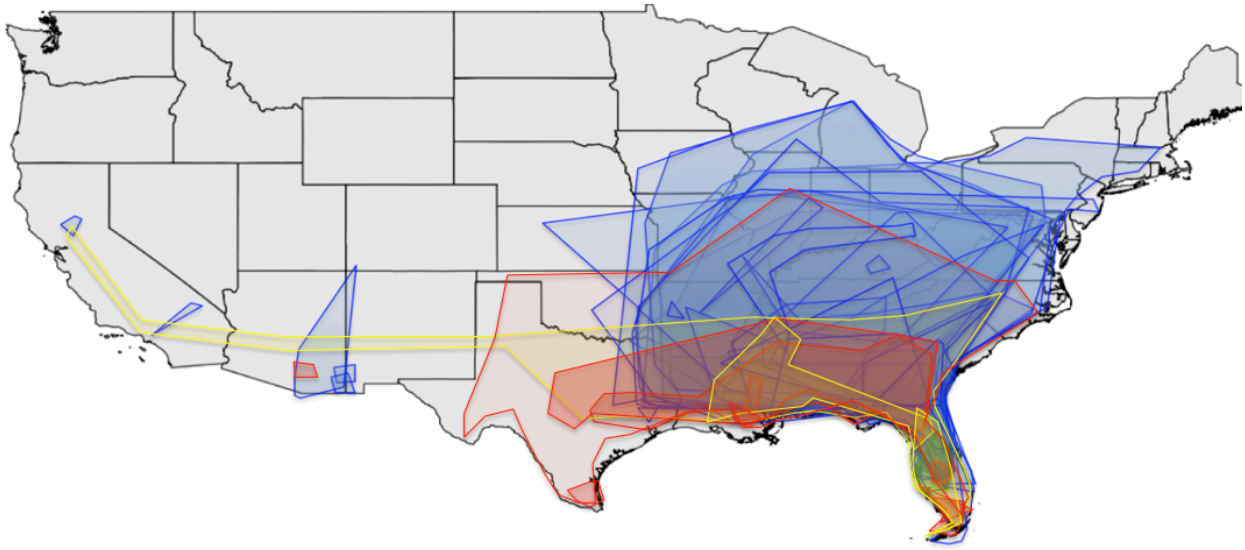


Figure. 4.2.

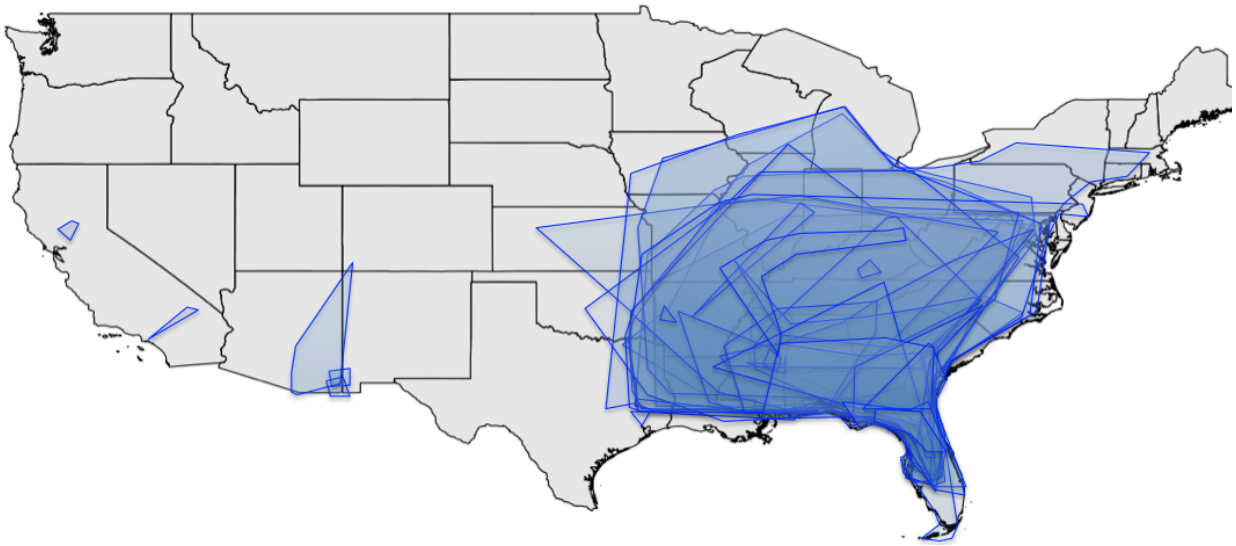
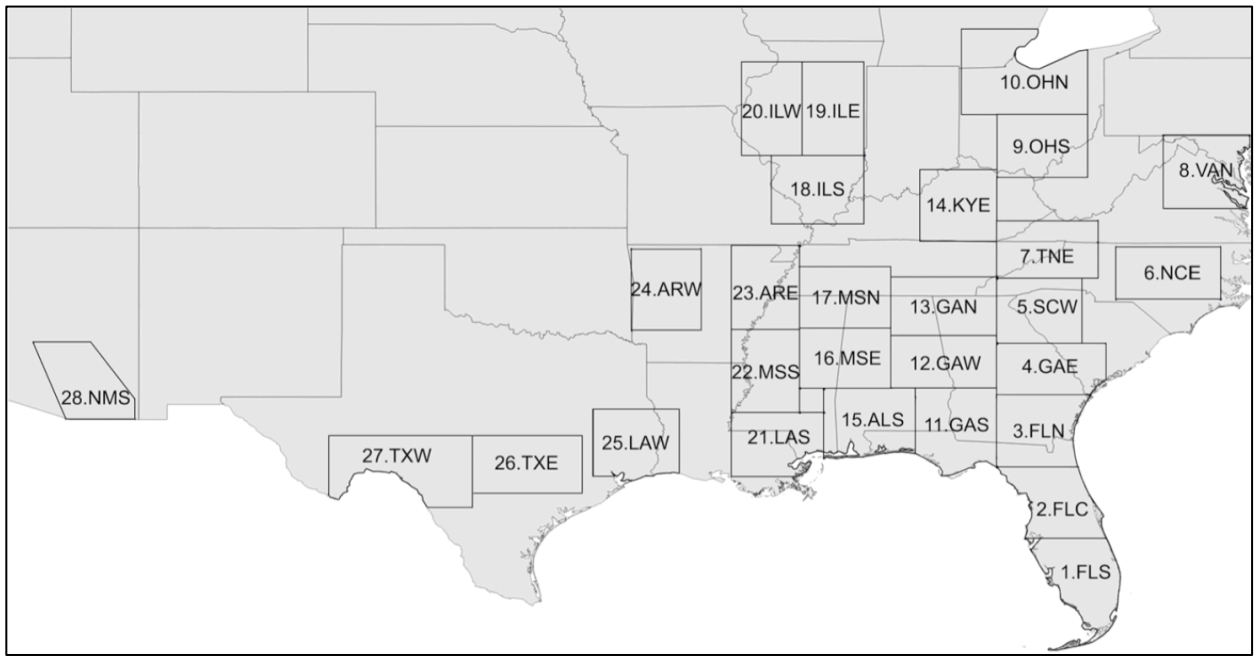


Figure 4.3.


10.OHN
20.ILW
19.ILE
9.OHS
8.VAN
18.ILS
14.KYE
7.TNE
6.NCE
24.ARW
23.ARE
17.MSN
13.GAN
5.SCW
16.MSE
12.GAW
4.GAE
22.MSS
28.NMS
15.ALS
11.GAS
3.FLN
25.LAW
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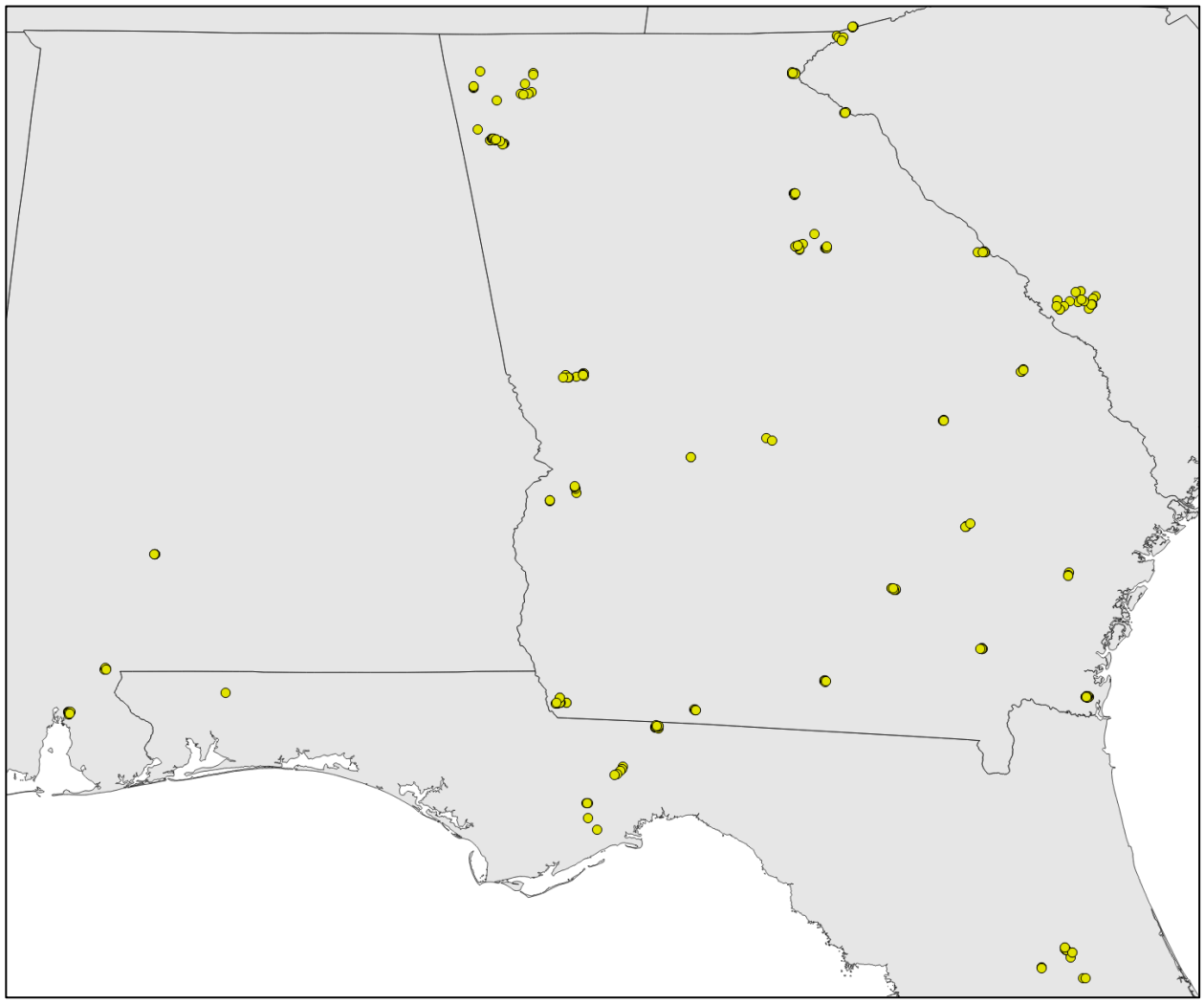
27.TXW
26.TXE
2.FLC
1.FLS

Figure 4.4.



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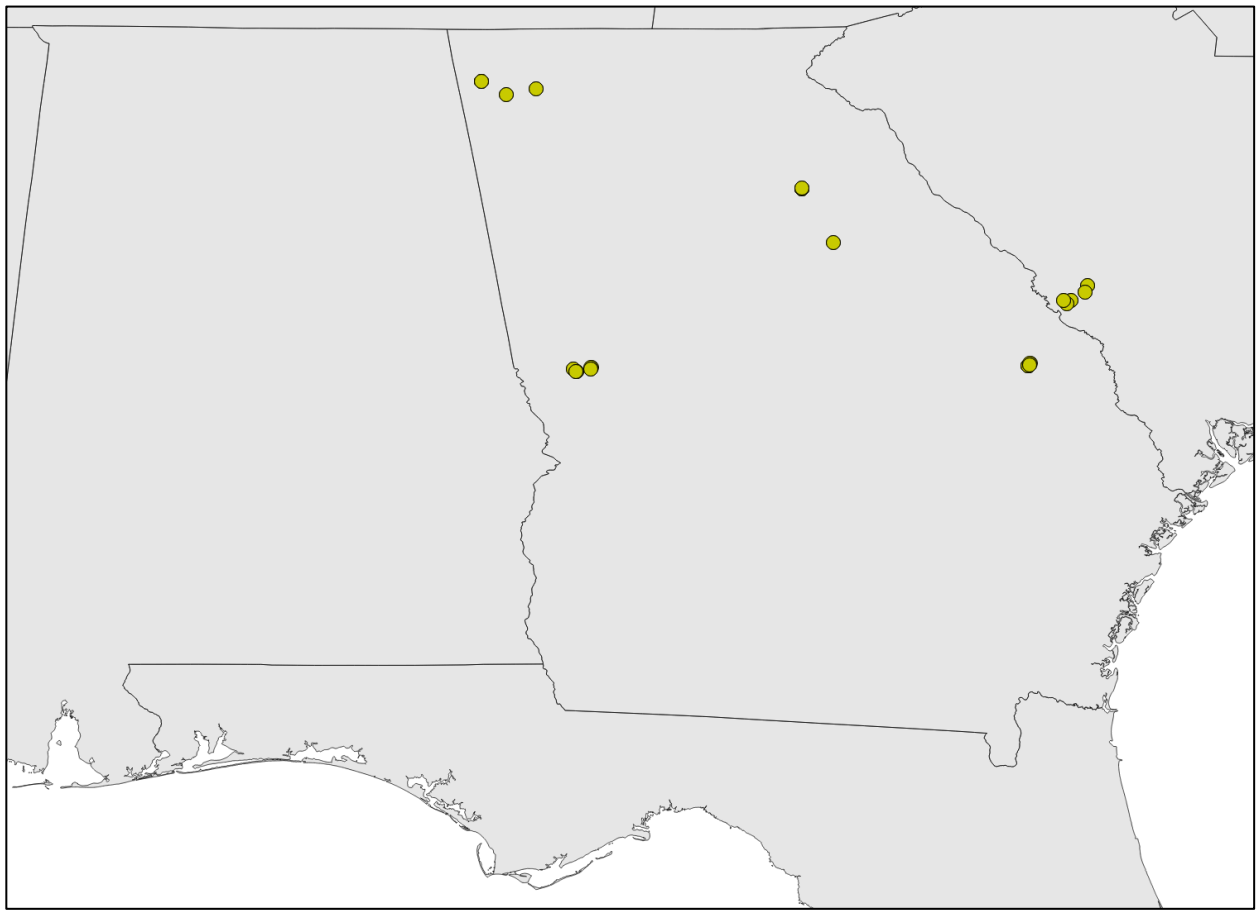

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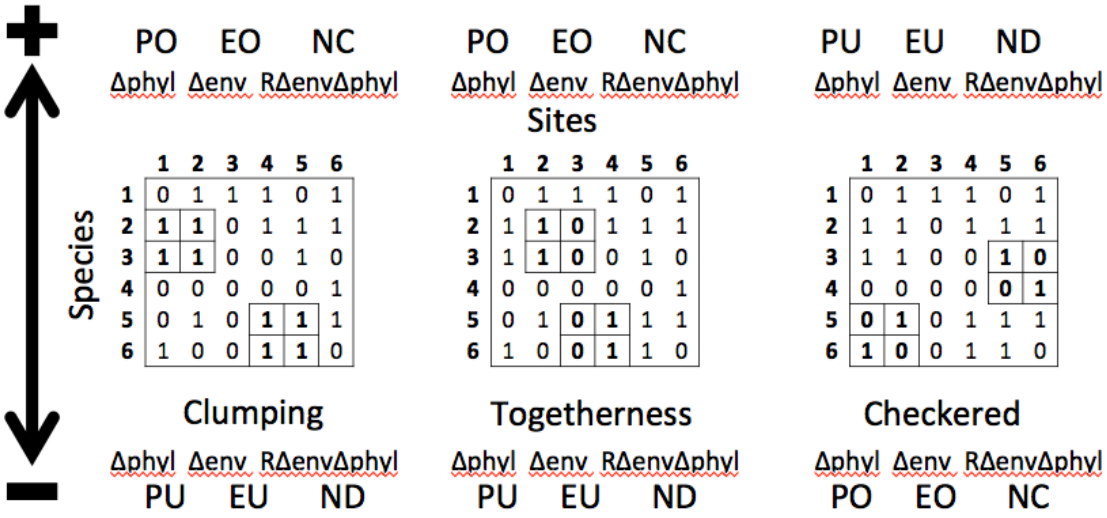


Figure 4.7.

	All Species			Nearctic Species		
Δphyl	**CL**	**TG**	**CK**	**CL**	**TG**	**CK**
Bioregion	(+/+/+)	(+/+/+)	(-/-/)	(-/-/-)	(-/-/)	
0.20 ha	(-)	(-)	(-)		(-)	(-)
25 m	(+)		(+)		(+)	
one m						

Figure 4.8.

All Species	CL	TG	CK	CL	TG	CK
	MAT			PDQ		
HF (Δenv)		(-/-/-)	(+/+/+)	(-/-/-)	(/+/+)	(/-/-)
PNC (RΔenvΔphyl)	(+/+/+)		(-/-/-)		(+/ /)	(/ /+)
Nearctic Clade Species	CL	TG	CK	CL	TG	CK
	MAT			PDQ		
HF (Δenv)			(+/ /)	(-/-/-)	(-/ /-)	(/+/)
PNC (RΔenvΔphyl)	(-/-/-)	(-/ /+)		(+/+/+)	(-/-/-)	(-/ /)

Figure 4.9.

All Species	CL	TG	CK	CL	TG	CK	CL	TG	CK	CL	TG	CK	CL	TG	CK
	LAT			ALT			MAT			PDQ			Shade		
HF (Δenv)	(-*)	(+*)					(+*)	(-*)							
PNC (RΔenvΔphyl)		(+**)	(-*)		(+*)	(-*)			(+*)		(+**)		(+**)	(+*)	
	LitterD			Bare			Litter			Plant			Stone		
HF (Δenv)	(+*)							(+*)	(-*)						
PNC (RΔenvΔphyl)												(-*)			(-*)

Nearctic Clade Species	CL	TG	CK	CL	TG	CK	CL	TG	CK	CL	TG	CK	CL	TG	CK
	LAT			ALT			MAT			PDQ			Shade		
HF (Δenv)	(-*)	(+**)	(-*)		(+*)	(-*)			(+*)		(+*)			(+*)	(-*)
PNC (RΔenvΔphyl)			(-*)			(-*)			(+*)			(-*)	(-*)	(+*)	
	LitterD			Bare			Litter			Plant			Stone		
HF (Δenv)					(-*)	(+*)			(-*)						
PNC (RΔenvΔphyl)		(-*)													

Figure 4.10.

	CL	TG	CK	CL	TG	CK	CL	TG	CK	CL	TG	CK	CL	TG	CK	CL	TG	CK
All Species	LAT			ALT			MAT			PDQ			SM			mLit		
HF (Δenv)	(+)	(-)		(+)			(-*)			(+**)			(+)					
PNC (RΔenvΔphyl)	(+*)			(-)												(-)		
	TreeS			Clay			Loose			Rocky			Sand			Tbase		
HF (Δenv)				(+**)									(-**)					
PNC (RΔenvΔphyl)	(-)					(-)							(-**)			(-)		
	vLit			StickS			StickL			nTree			DBH			HW		
HF (Δenv)	(+)			(-)						(-)			(+*)		(+*)	(+)		
PNC (RΔenvΔphyl)	(-)						(+)											
	Branch			Rock			Dep.			Log			Open			Stump		
HF (Δenv)										(+**)			(-)	(-*)		(+)	(-)	
PNC (RΔenvΔphyl)							(-)											
	CL	TG	CK	CL	TG	CK	CL	TG	CK	CL	TG	CK	CL	TG	CK	CL	TG	CK
Nearctic species	LAT			ALT			MAT			PDQ			SM			mLit		
HF (Δenv)				(+**)	(+*)					(+)			(+)			(+**)		
PNC (RΔenvΔphyl)	(-**)	(-*)		(+)			(+*)				(-)		(+*)			(+**)		
	TreeS			Clay			Loose			Rocky			Sand			Tbase		
HF (Δenv)							(+)			(+)						(+)		
PNC (RΔenvΔphyl)							(-**)						(+*)			(+**)	(-)	
	vLit			StickS			StickL			nTree			DBH			HW		
HF (Δenv)	(+**)			(-**)									(-*)	(+)		(+)		
PNC (RΔenvΔphyl)							(+**)						(+)					
	Branch			Rock			Dep.			Log			Open			Stump		
HF (Δenv)	(+)									(+)			(-*)			(+*)		
PNC (RΔenvΔphyl)		(+)								(-**)			(+*)					

Figure 4.11.

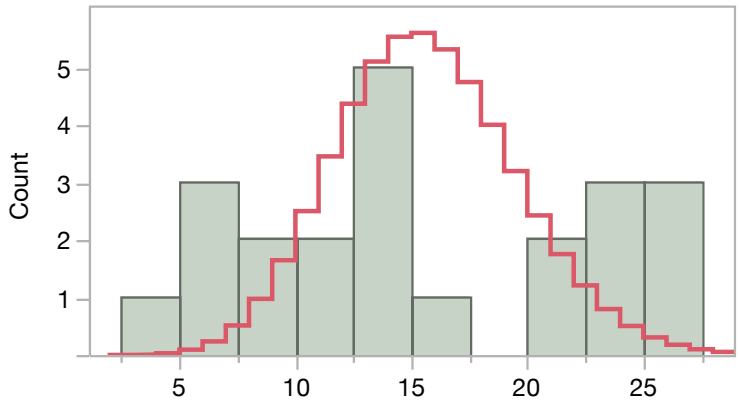
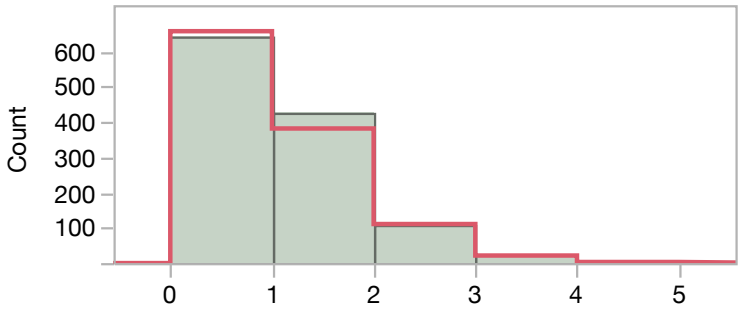


Figure 4.12.



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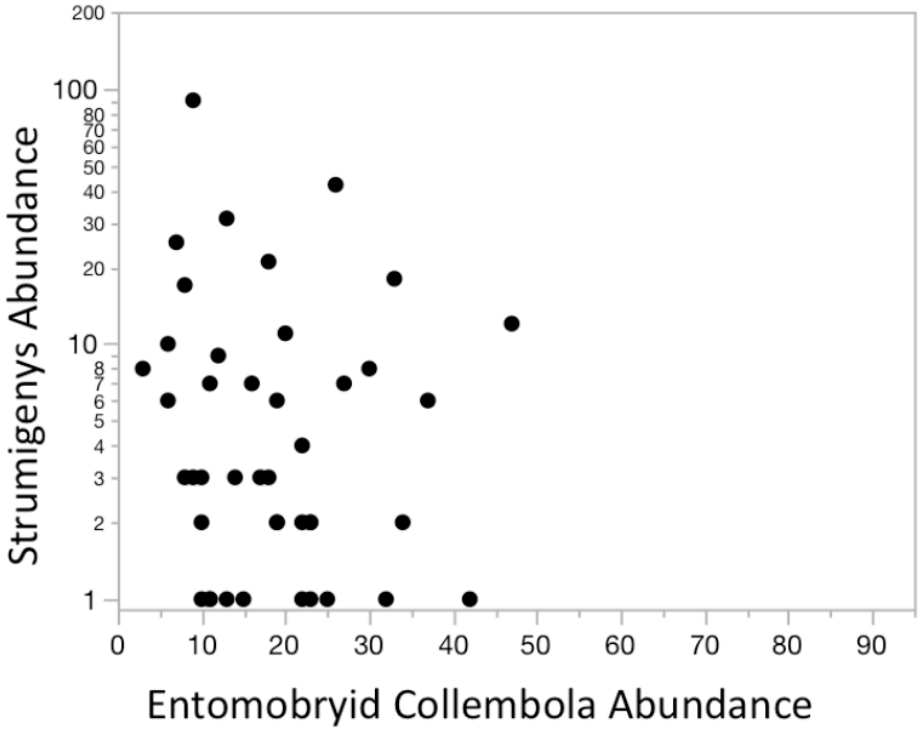
Strumigenys Abundance
200
100
80
70
60
50
40
30
20
10
8
7
6
5
4
3
2
1
0
10
20
30
40
50
60
70
80
90
Entomobryid Collembola Abundance

Figure 4.14.

Level-1. All Species								
	Clumping		Togetherness		Checkered			
	MAT	PDQ	MAT	PDQ	MAT	PDQ		
Δenv	(-1.0/0.1/1.2)	**(6.3/6.7/3.6)**	**(6.0/4.1/4.3)**	(-1.9/**-2.2/-4.2**)	**(3.8/3.0/4.8)**	(-1.3/**-2.1/-4.0**)		
RΔenvΔphyl	**(9.4/8.6/5.8)**	(1.8/-0.3/-0.2)	(-0.2/-0.1/-0.2)	**(2.1**/1.3/-1.6)	**(2.6/3.5/3.6)**	(-1.3/0.3/**-2.4**)		
Δphyl	**(-11.3/-9.3/-10.0)**		**(-7.7/-5.6/-3.4)**		(-1.0/**-2.6/-4.2**)			
Δenv		**EO*** **	**EO*** **	**EU****	**EU*** **	**EO****		
RΔenvΔphyl	**NC*** **			NC*	**ND*** **	**NC***		
Δphyl	**PU*** **		**PU*** **		**PO****			
Level-2. Nearctic Species								
	Clumping		Togetherness		Checkered			
	MAT	PDQ	MAT	PDQ	MAT	PDQ		
Δenv	(-0.8/0.8/0.0)	**(4.5/5.8/5.7)**	(-0.2/1.9/1.4)	**(-5.5**/-1.7/**-2.5)**	**(2.3**/1.4/1.6)	(-1.8/**2.9**/0.8)		
RΔenvΔphyl	**(-4.2/-4.2/-7.6)**	**(3.6/5.7/3.3)**	**(-3.3**/-1.0/**2.7)**	**(-3.3/-2.8/-1.6)**	(0.3/1.3/0.1)	**(3.4**/-1.8/-1.2**)**		
Δphyl	**(9.8/10.6/10.2)**		**(4.8/5.0**/0.8)		(1.1/1.8/2.0)			
Δenv		**EO*** **		**EU****	EU*	EU*		
RΔenvΔphyl	**ND*** **	**NC*** **	ND*/NC*	**ND*** **		ND*		
Δphyl	**PO*** **		**PO****					

Figure 4.15.

	LAT	ALT	Shade	LitterD	Bare	Litter	Plant	Stone	MAT	PDQ
Level-1. All Species										
Δenv	**(EO*,EU*,-)**			**(EU*,-,-)**		**(EU*,-,EO*)**			**(EU*,EO,-)**	
RΔenvΔphyl	**(NC**,ND*,-)**	**(-,NC*,ND*)**	**(NC**,NC*,-)**				**(-,-,ND*)**	**(-,-,ND*)**	**(-,-,NC**)**	**(-,NC**,-)**
Δphyl	**(PO*,PO*,PO*)**									
Level-2. Nearctic species										
Δenv	**(EO*,EU**,EO**)**	**(-,EU*,EO*)**	**(-,EU*,EO*)**		**(-,EO*,EU*)**	**(-,-,EO*)**			**(-,-,EU*)**	**(-,EU*,-)**
RΔenvΔphyl	**(-,-,ND*)**	**(-,-,ND*)**	**(NC*,NC*,-)**	**(-ND*,-)**					**(-,-,NC*)**	**(-,-,ND*)**
Δphyl	**(-,PO*,PO*)**									

Figure 4.16.

						Nest Site Availability				Tree Community			
	Occ.	LAT	ALT	MAT	PDQ	SM	mLit	vLit	StickS	StickL	nTree	DBH	HW	TreeS
Level-1. All Species														
Δenv		(EU,EO,-)	(EU,-,-)	(EO*,-,-)	(EU**,-,-)	(-,EU,-)		(EU,-,-)	(EO,-,-)		(EO,-,-)	(EU*,-,EU*)	(-,EU,-)	
RΔenvΔphyl		(NC*,-,-)	(ND,-,-)				(-,ND,-)	(ND,-,-)		(-,NC,-)				(ND,-,-)
Δphyl	(PU**,-,PU*)													
Level-2. Nearctic species														
Δenv			(EU**,EU*,-)		(EU,-,-)	(-,EU,-)	(EU**,-,-)	(EU**,-,-)	(EO**,-,-)			(-,EO*,EU)	(-,EU,-)	
RΔenvΔphyl		(ND**,ND*,-)	(NC,-,-)	(-,NC*,-)	(-,ND,-)	(NC*,-,-)	(NC**,-,-)			(NC**,-,-)		(-,NC,-)		
Δphyl	(-,PU,-)													

	Soil			Ground Coverage						
	Clay	Loose	Rocky	Sand	Tbase	Branch	Rock	Dep.	Log	Open	Stump
Level-1. All Species											
Δenv	(EU**,-,-)			(EO**,-,-)					(EU**,-,-)	(EO,EO*,-)	(-,EU,-)
RΔenvΔphyl	(-,-,ND)			(ND**,-,-)	(ND,-,-)			(ND,-,-)			
Level-2. Nearctic species		(EU,-,-)	(EU,-,-)		(-,EU,-)	(-,EU,-)			(EU,-,-)	(-,EO*,-)	(-,EU*,EO)
Δenv		(ND**,-,-)		(NC*,-,-)	(NC**,ND,-)	(-,-,NC)			(ND**,-,-)	(-,NC*,-)	
RΔenvΔphyl											

Table 4.1.

Geographic Scale	Range Examined km2	Site Size	Nearctic Sp.	Other Sp.	MAT max	MAT min	MAT mean SD	PDQ max	PDQ min	PDQ mean SD
Local Communities	55,359	25 m^2	19	4	17.8	13.5	16.5±1.3	311	221	250.0±29.4
Regional Communities	301,506	0.20 ha	24	8	21.2	12.5	17.5±2.2	442	185	257.1±54.3
Bioregions	5,105,904,792,780	60,000 km^2	40	16	26.7	6	17.6±3.3	447	4	243.0±54.0

Table 4.2.

Matrix 1	Matrix 2	R^2	*p*-value
Geographic Distance	Tree Species	0.17	< 0.001
Geographic Distance	All *Strumigenys* species	0.16	< 0.001
Geographic Distance	Nearctic clade *Strumigenys*	0.16	< 0.001
Tree Species	All *Strumigenys* species	0.40	< 0.001
Tree Species	Nearctic clade *Strumigenys*	0.40	< 0.001

Table 4.3.

Metric	MCR-all	MCR-Nea	Variable1	Variable2	Z-All	p-All	Z-Nea	p-Nea
Clumping	13	1	Species Occ.	Phyl Dist	**-11.3**	**<0.001**	**9.83**	**<0.001**
Together	13	1	Species Occ.	Phyl Dist	**-7.66**	**<0.001**	**4.76**	**<0.001**
Checkered	13	1	Species Occ.	Phyl Dist	-1.02	0.306	1.12	0.264
Clumping	13	1	MAT	Phyl Dist	**9.39**	**<0.001**	**-4.16**	**<0.001**
Together	13	1	MAT	Phyl Dist	-0.23	0.820	**-3.28**	**<0.001**
Checkered	13	1	MAT	Phyl Dist	2.61	0.009	0.34	0.736
Clumping	13	1	MAT	EnvVar	-0.96	0.335	-0.79	0.428
Together	13	1	MAT	EnvVar	**5.99**	**<0.001**	-0.23	0.817
Checkered	13	1	MAT	EnvVar	**3.81**	**<0.001**	**2.32**	**0.020**
Clumping	13	1	PDQ	Phyl Dist	1.77	0.077	3.62	**<0.001**
Together	13	1	PDQ	Phyl Dist	2.07	0.038	-3.31	**<0.001**
Checkered	13	1	PDQ	Phyl Dist	-1.33	0.183	3.40	**<0.001**
Clumping	13	1	PDQ	EnvVar	**6.26**	**<0.001**	**4.55**	**<0.001**
Together	13	1	PDQ	EnvVar	-1.93	0.053	**-5.48**	**<0.001**
Checkered	13	1	PDQ	EnvVar	-1.27	0.202	**-1.78**	**0.074**
Clumping	55	40	Species Occ.	Phyl Dist	**-9.31**	**<0.001**	**10.65**	**<0.001**
Together	55	40	Species Occ.	Phyl Dist	**-5.64**	**<0.001**	**5.01**	**<0.001**
Checkered	55	40	Species Occ.	Phyl Dist	**-2.55**	0.0106382	1.75	0.0805415
Clumping	55	40	MAT	Phyl Dist	**8.63**	**<0.001**	**-4.16**	**<0.001**
Together	55	40	MAT	Phyl Dist	-0.12	0.906	-1.03	0.302
Checkered	55	40	MAT	Phyl Dist	**3.52**	**<0.001**	1.30	0.193
Clumping	55	40	MAT	EnvVar	0.10	0.922	0.79	0.432
Together	55	40	MAT	EnvVar	**4.12**	**<0.001**	1.92	0.054
Checkered	55	40	MAT	EnvVar	**3.02**	0.002	1.43	0.154
Clumping	55	40	PDQ	Phyl Dist	-0.30	0.762	**5.81**	**<0.001**
Together	55	40	PDQ	Phyl Dist	1.26	0.209	-1.65	0.099
Checkered	55	40	PDQ	Phyl Dist	0.32	0.750	**2.85**	0.004
Clumping	55	40	PDQ	EnvVar	**6.73**	**<0.001**	**5.72**	**<0.001**
Together	55	40	PDQ	EnvVar	**-2.18**	0.029	**-2.79**	0.005
Checkered	55	40	PDQ	EnvVar	**-2.05**	0.040	-1.76	0.078
Clumping	100	100	Species Occ.	Phyl Dist	**-9.98**	**<0.001**	**10.29**	**<0.001**
Together	100	100	Species Occ.	Phyl Dist	**-3.36**	**<0.001**	0.76	0.446
Checkered	100	100	Species Occ.	Phyl Dist	**-4.18**	**<0.001**	**1.96**	0.049
Clumping	100	100	MAT	Phyl Dist	**5.79**	**<0.001**	**-7.56**	**<0.001**
Together	100	100	MAT	Phyl Dist	-0.23	0.820	**2.69**	0.007
Checkered	100	100	MAT	Phyl Dist	**3.58**	**<0.001**	0.13	0.900
Clumping	100	100	MAT	EnvVar	1.22	0.221	0.03	0.975
Together	100	100	MAT	EnvVar	**4.32**	**<0.001**	1.44	0.151
Checkered	100	100	MAT	EnvVar	**4.80**	**<0.001**	1.56	0.119
Clumping	100	100	PDQ	Phyl Dist	-0.26	0.798	**5.69**	**<0.001**
Together	100	100	PDQ	Phyl Dist	-1.61	0.106	**-2.48**	0.013
Checkered	100	100	PDQ	Phyl Dist	**-2.43**	0.015	0.78	0.434
Clumping	100	100	PDQ	EnvVar	**3.60**	**<0.001**	**3.26**	**<0.001**
Together	100	100	PDQ	EnvVar	**-4.16**	**<0.001**	-1.60	0.109
Checkered	100	100	PDQ	EnvVar	**-3.98**	**<0.001**	-1.20	0.232

Table 4.4. (continued)

Metric	Variable1	Variable2	Z-All	p-All	Z-Nearctic	p-Nearctic
Clumping	Species	Phyl Dist	**2.41**	**0.016**	1.46	0.145
Together	Species	Phyl Dist	**2.81**	**0.005**	**2.54**	**0.011**
Checkered	Species	Phyl Dist	**-2.4**	**0.016**	**-2.77**	**0.006**
Clumping	Shade	Phyl Dist	**3.54**	**< 0.001**	**2.05**	**0.04**
Together	Shade	Phyl Dist	**2.08**	**0.037**	**2.12**	**0.034**
Checkered	Shade	Phyl Dist	-0.23	0.817	0.86	0.391
Clumping	Shade	EnvVar	0.83	0.408	1.75	0.08
Together	Shade	EnvVar	-1.48	0.14	**-2.24**	**0.025**
Checkered	Shade	EnvVar	-1.38	0.166	**-2.55**	**0.011**
Clumping	LAT	Phyl Dist	**3.23**	**0.001**	1.22	0.224
Together	LAT	Phyl Dist	0.77	0.442	1.63	0.102
Checkered	LAT	Phyl Dist	**2.06**	**0.039**	**2.26**	**0.023**
Clumping	LAT	EnvVar	**3.02**	**0.002**	**2.05**	**0.04**
Together	LAT	EnvVar	**-1.97**	**0.049**	**-3.52**	**< 0.001**
Checkered	LAT	EnvVar	-1.66	0.097	**-3.55**	**< 0.001**
Clumping	ALT	Phyl Dist	**2.39**	**0.017**	-0.47	0.636
Together	ALT	Phyl Dist	1.17	0.24	-0.09	0.932
Checkered	ALT	Phyl Dist	**2.97**	**0.003**	**2.99**	**0.003**
Clumping	ALT	EnvVar	0.39	0.695	1.19	0.233
Together	ALT	EnvVar	0.63	0.526	**-2.65**	**0.008**
Checkered	ALT	EnvVar	0.74	0.46	**-2.7**	0.007
Clumping	SM	Phyl Dist	1.76	0.079	1.71	0.087
Together	SM	Phyl Dist	0.27	0.791	1.72	0.085
Checkered	SM	Phyl Dist	0.79	0.428	1.69	0.09
Clumping	SM	EnvVar	0.82	0.413	0.8	0.423
Together	SM	EnvVar	-0.65	0.515	-0.42	0.678
Checkered	SM	EnvVar	-0.53	0.597	-0.36	0.72
Clumping	pH	Phyl Dist	-0.51	0.609	-0.55	0.582
Together	pH	Phyl Dist	-0.91	0.361	-0.17	0.865
Checkered	pH	Phyl Dist	-0.23	0.82	0.27	0.784
Clumping	pH	EnvVar	1.4	0.162	1.19	0.234
Together	pH	EnvVar	-0.58	0.56	-0.86	0.391
Checkered	pH	EnvVar	-0.43	0.671	-0.67	0.503
Clumping	mLit	Phyl Dist	0.37	0.711	-1.03	0.301
Together	mLit	Phyl Dist	-0.32	0.751	**-1.98**	**0.048**
Checkered	mLit	Phyl Dist	1.53	0.126	-0.99	0.322
Clumping	mLit	EnvVar	**-2.19**	**0.028**	-1.17	0.241
Together	mLit	EnvVar	1.24	0.216	1.22	0.222
Checkered	mLit	EnvVar	1.24	0.214	1.02	0.306
Clumping	cBare	Phyl Dist	-1.52	0.128	-0.92	0.36
Together	cBare	Phyl Dist	-1.67	0.094	-0.74	0.461
Checkered	cBare	Phyl Dist	0.54	0.587	-0.44	0.659
Clumping	cBare	EnvVar	-0.25	0.806	-1.18	0.239
Together	cBare	EnvVar	0.99	0.321	**2.15**	**0.032**
Checkered	cBare	EnvVar	1	0.317	**2.2**	**0.028**
Clumping	cLit	Phyl Dist	0.72	0.471	0.57	0.571
Together	cLit	Phyl Dist	1.61	0.108	0.87	0.386
Checkered	cLit	Phyl Dist	-1.39	0.164	0.73	0.466
Clumping	cLit	EnvVar	0.74	0.46	0.72	0.472
Together	cLit	EnvVar	**-2.2**	**0.028**	-1.78	0.075
Checkered	cLit	EnvVar	**-2.25**	**0.024**	**-1.98**	**0.048**

Metric	Variable1	Variable2	Z-All	p-All	Z-Nearctic	p-Nearctic
Clumping	cStone	Phyl Dist	1.45	0.146	0.83	0.406
Together	cStone	Phyl Dist	1.25	0.211	0.44	0.664
Checkered	cStone	Phyl Dist	3.06	0.002	-0.52	0.602
Clumping	cStone	EnvVar	0.81	0.42	0.81	0.419
Together	cStone	EnvVar	-0.14	0.893	-1.27	0.203
Checkered	cStone	EnvVar	-0.09	0.925	-1.31	0.191
Clumping	cPlant	Phyl Dist	-1	0.32	-0.79	0.428
Together	cPlant	Phyl Dist	-1.69	0.091	-0.82	0.415
Checkered	cPlant	Phyl Dist	0.03	0.976	-0.41	0.683
Clumping	cPlant	EnvVar	-1.06	0.289	-0.61	0.539
Together	cPlant	EnvVar	1.86	0.063	1.61	0.108
Checkered	cPlant	EnvVar	**1.98**	**0.047**	1.79	0.073
Clumping	cWater	Phyl Dist	-0.82	0.414	-1.04	0.298
Together	cWater	Phyl Dist	-0.83	0.405	-1.02	0.31
Checkered	cWater	Phyl Dist	-0.19	0.847	-0.99	0.324
Clumping	cWater	EnvVar	-0.92	0.358	-0.79	0.43
Together	cWater	EnvVar	1.05	0.295	1.24	0.216
Checkered	cWater	EnvVar	0.88	0.377	1.17	0.241
Clumping	MAT	Phyl Dist	-1.14	0.253	1.05	0.293
Together	MAT	Phyl Dist	-0.48	0.635	1.03	0.301
Checkered	MAT	Phyl Dist	**-3.58**	**< 0.001**	**-2.29**	**0.022**
Clumping	MAT	EnvVar	**-2.02**	**0.043**	-0.93	0.352
Together	MAT	EnvVar	**2.43**	**0.015**	1.69	0.091
Checkered	MAT	EnvVar	0.54	0.59	**2.62**	**0.009**
Clumping	PDQ	Phyl Dist	**3.62**	**< 0.001**	0.4	0.693
Together	PDQ	Phyl Dist	1.59	0.112	0.43	0.664
Checkered	PDQ	Phyl Dist	1.33	0.185	**2.35**	**0.019**
Clumping	PDQ	EnvVar	-0.72	0.472	0.94	0.347
Together	PDQ	EnvVar	1.61	0.107	**-1.98**	**0.047**
Checkered	PDQ	EnvVar	1.52	0.127	-1.82	0.069

Table 4.5.

Metric	Variable1	Variable2	Z-All	p-All	Z-Nearctic	p-Nearctic
Clumping	Species Occ.	Phyl Dist	**-9.30**	**< 0.001**	-0.01	0.990
Together	Species Occ.	Phyl Dist	0.30	0.767	**-2.21**	**0.027**
Checkered	Species Occ.	Phyl Dist	**2.79**	**0.005**	1.66	0.097
Clumping	LAT	Phyl Dist	**2.69**	**0.007**	**-5.27**	**< 0.001**
Together	LAT	Phyl Dist	-0.69	0.491	**-2.81**	**0.005**
Checkered	LAT	Phyl Dist	0.18	0.854	-0.17	0.868
Clumping	LAT	EnvVar	**-2.44**	**0.014**	0.11	0.910
Together	LAT	EnvVar	**2.09**	**0.036**	0.54	0.590
Checkered	LAT	EnvVar	1.58	0.113	1.33	0.183
Clumping	ALT	Phyl Dist	**-2.44**	**0.014**	**2.53**	**0.011**
Together	ALT	Phyl Dist	-1.78	0.075	-1.83	0.067
Checkered	ALT	Phyl Dist	0.38	0.706	-0.01	0.992
Clumping	ALT	EnvVar	**-2.33**	**0.020**	**-3.53**	**< 0.001**
Together	ALT	EnvVar	-1.62	0.105	**-2.72**	**0.006**
Checkered	ALT	EnvVar	-0.82	0.413	-0.66	0.509
Clumping	MAT	Phyl Dist	0.85	0.395	0.86	0.392
Together	MAT	Phyl Dist	1.78	0.075	**2.92**	**0.003**
Checkered	MAT	Phyl Dist	-0.34	0.732	0.16	0.871
Clumping	MAT	EnvVar	**2.70**	**0.007**	1.87	0.061
Together	MAT	EnvVar	0.62	0.538	1.55	0.121
Checkered	MAT	EnvVar	-0.19	0.852	-0.16	0.874
Clumping	PDQ	Phyl Dist	-0.67	0.503	-0.66	0.509
Together	PDQ	Phyl Dist	-1.41	0.157	**-2.53**	**0.011**
Checkered	PDQ	Phyl Dist	0.64	0.523	0.15	0.880
Clumping	PDQ	EnvVar	**-3.41**	**< 0.001**	**-2.29**	**0.022**
Together	PDQ	EnvVar	-0.54	0.593	-1.48	0.138
Checkered	PDQ	EnvVar	0.23	0.822	0.04	0.970
Clumping	SM	Phyl Dist	-1.12	0.263	**2.73**	**0.006**
Together	SM	Phyl Dist	0.73	0.465	-1.14	0.253
Checkered	SM	Phyl Dist	0.81	0.416	-0.54	0.591
Clumping	SM	EnvVar	-0.03	0.977	-1.25	0.210
Together	SM	EnvVar	**-2.18**	**0.029**	**-2.27**	**0.023**
Checkered	SM	EnvVar	-1.00	0.316	-1.80	0.071
Clumping	mLit	Phyl Dist	**-2.31**	**0.021**	**3.18**	**0.001**
Together	mLit	Phyl Dist	-0.06	0.949	-0.82	0.410
Checkered	mLit	Phyl Dist	-1.40	0.162	0.94	0.347
Clumping	mLit	EnvVar	-1.84	0.066	**-4.23**	**< 0.001**
Together	mLit	EnvVar	-0.11	0.914	-0.49	0.628
Checkered	mLit	EnvVar	-0.70	0.486	0.31	0.756
Clumping	vLit	Phyl Dist	**-2.20**	**0.028**	1.60	0.110
Together	vLit	Phyl Dist	-1.60	0.110	-0.68	0.494
Checkered	vLit	Phyl Dist	-0.42	0.672	0.78	0.433
Clumping	vLit	EnvVar	**-2.09**	**0.036**	**-3.59**	**< 0.001**
Together	vLit	EnvVar	-0.48	0.631	-0.49	0.628
Checkered	vLit	EnvVar	-0.93	0.355	-0.12	0.906
Clumping	SticksS	Phyl Dist	0.53	0.597	-0.74	0.460
Together	SticksS	Phyl Dist	0.19	0.850	0.40	0.687
Checkered	SticksS	Phyl Dist	1.33	0.182	-0.43	0.665
Clumping	SticksS	EnvVar	**2.28**	**0.023**	**3.93**	**< 0.001**
Together	SticksS	EnvVar	0.05	0.964	0.26	0.797
Checkered	SticksS	EnvVar	0.21	0.835	-0.31	0.758

Metric	Variable1	Variable2	Z-All	p-All	Z-Nearctic	p-Nearctic
Clumping	SticksL	Phyl Dist	1.45	0.147	**3.32**	**< 0.001**
Together	SticksL	Phyl Dist	**2.67**	**0.007**	-1.17	0.241
Checkered	SticksL	Phyl Dist	0.39	0.700	-0.38	0.707
Clumping	SticksL	EnvVar	-0.99	0.324	1.58	0.113
Together	SticksL	EnvVar	-0.09	0.929	-0.93	0.355
Checkered	SticksL	EnvVar	0.19	0.851	-0.59	0.556
Clumping	Clay	Phyl Dist	0.42	0.678	0.63	0.530
Together	Clay	Phyl Dist	0.75	0.452	-1.02	0.306
Checkered	Clay	Phyl Dist	**2.50**	**0.012**	-1.54	0.123
Clumping	Clay	EnvVar	**-3.50**	**< 0.001**	-1.95	0.051
Together	Clay	EnvVar	0.85	0.398	0.53	0.595
Checkered	Clay	EnvVar	1.13	0.260	-0.40	0.693
Clumping	Loose	Phyl Dist	1.29	0.197	**-2.72**	**0.006**
Together	Loose	Phyl Dist	0.02	0.985	0.31	0.755
Checkered	Loose	Phyl Dist	-0.96	0.338	0.43	0.666
Clumping	Loose	EnvVar	-0.56	0.578	**-2.24**	**0.025**
Together	Loose	EnvVar	-0.69	0.489	-0.32	0.750
Checkered	Loose	EnvVar	-0.57	0.570	0.33	0.740
Clumping	Rocky	Phyl Dist	-1.78	0.075	-0.90	0.367
Together	Rocky	Phyl Dist	-1.39	0.166	-0.98	0.327
Checkered	Rocky	Phyl Dist	0.94	0.349	-0.01	0.990
Clumping	Rocky	EnvVar	-1.10	0.269	**-2.10**	**0.035**
Together	Rocky	EnvVar	-0.54	0.589	-0.64	0.520
Checkered	Rocky	EnvVar	-0.75	0.455	-0.58	0.565
Clumping	Sand	Phyl Dist	**-5.69**	**< 0.001**	**2.64**	**0.008**
Together	Sand	Phyl Dist	-1.55	0.122	1.72	0.085
Checkered	Sand	Phyl Dist	-0.62	0.538	-0.30	0.766
Clumping	Sand	EnvVar	**3.79**	**< 0.001**	0.48	0.631
Together	Sand	EnvVar	-0.38	0.701	0.27	0.791
Checkered	Sand	EnvVar	-0.94	0.347	-0.26	0.797
Clumping	Tbase	Phyl Dist	**-2.37**	**0.018**	**3.80**	**< 0.001**
Together	Tbase	Phyl Dist	1.72	0.085	**-2.00**	**0.045**
Checkered	Tbase	Phyl Dist	1.31	0.191	-1.92	0.055
Clumping	Tbase	EnvVar	0.06	0.950	0.40	0.688
Together	Tbase	EnvVar	-1.12	0.265	**-2.08**	**0.037**
Checkered	Tbase	EnvVar	-0.66	0.508	-1.83	0.067
Clumping	Branch	Phyl Dist	1.15	0.252	1.94	0.052
Together	Branch	Phyl Dist	0.01	0.992	-1.46	0.144
Checkered	Branch	Phyl Dist	0.01	0.995	**-2.18**	**0.029**
Clumping	Branch	EnvVar	-1.42	0.156	-0.54	0.590
Together	Branch	EnvVar	-1.54	0.123	**-2.37**	**0.018**
Checkered	Branch	EnvVar	-0.61	0.544	-0.45	0.653
Clumping	Rock	Phyl Dist	-1.22	0.222	0.09	0.927
Together	Rock	Phyl Dist	0.33	0.738	-0.08	0.933
Checkered	Rock	Phyl Dist	0.84	0.399	-0.43	0.665
Clumping	Rock	EnvVar	-0.70	0.484	-1.95	0.051
Together	Rock	EnvVar	-0.97	0.331	-0.70	0.486
Checkered	Rock	EnvVar	-1.18	0.240	-1.11	0.268
Clumping	Dep.	Phyl Dist	**-2.09**	**0.036**	0.91	0.365
Together	Dep.	Phyl Dist	-1.07	0.283	0.99	0.322
Checkered	Dep.	Phyl Dist	1.04	0.297	-0.04	0.971
Clumping	Dep.	EnvVar	0.42	0.677	-0.70	0.487

Metric	Variable1	Variable2	Z-All	p-All	Z-Nearctic	p-Nearctic
Together	Dep.	EnvVar	-1.69	0.090	-1.51	0.132
Checkered	Dep.	EnvVar	-1.30	0.195	-0.90	0.368
Clumping	Log	Phyl Dist	-0.66	0.512	**-5.41**	**< 0.001**
Together	Log	Phyl Dist	-1.09	0.277	-1.33	0.183
Checkered	Log	Phyl Dist	0.87	0.384	-0.43	0.669
Clumping	Log	EnvVar	**-4.68**	**< 0.001**	**-2.15**	**0.032**
Together	Log	EnvVar	1.14	0.255	0.88	0.379
Checkered	Log	EnvVar	1.76	0.078	1.43	0.153
Clumping	Open	Phyl Dist	0.83	0.408	0.56	0.579
Together	Open	Phyl Dist	0.39	0.695	**3.12**	**0.002**
Checkered	Open	Phyl Dist	-0.75	0.455	1.00	0.318
Clumping	Open	EnvVar	**2.04**	**0.041**	1.01	0.311
Together	Open	EnvVar	**2.56**	**0.010**	**3.04**	**0.002**
Checkered	Open	EnvVar	1.30	0.195	1.57	0.116
Clumping	Stump	Phyl Dist	-1.50	0.133	1.14	0.253
Together	Stump	Phyl Dist	-1.52	0.127	-1.17	0.242
Checkered	Stump	Phyl Dist	0.30	0.767	0.51	0.610
Clumping	Stump	EnvVar	1.18	0.238	-0.33	0.745
Together	Stump	EnvVar	**-2.54**	**0.011**	**-3.45**	**< 0.001**
Checkered	Stump	EnvVar	**-1.96**	**0.049**	-1.46	0.144
Clumping	nTree	Phyl Dist	-1.09	0.274	-0.97	0.332
Together	nTree	Phyl Dist	-0.26	0.794	-1.40	0.160
Checkered	nTree	Phyl Dist	-0.80	0.423	-0.01	0.995
Clumping	nTree	EnvVar	**2.25**	**0.024**	1.86	0.063
Together	nTree	EnvVar	-0.62	0.533	-0.81	0.418
Checkered	nTree	EnvVar	-1.43	0.152	-1.55	0.121
Clumping	DBH	Phyl Dist	1.05	0.295	-1.55	0.121
Together	DBH	Phyl Dist	0.14	0.888	**2.04**	**0.041**
Checkered	DBH	Phyl Dist	1.12	0.264	-1.27	0.203
Clumping	DBH	EnvVar	**-2.86**	**0.004**	-1.51	0.131
Together	DBH	EnvVar	1.86	0.063	**2.32**	**0.020**
Checkered	DBH	EnvVar	**2.64**	**0.008**	**2.00**	**0.045**
Clumping	HW	Phyl Dist	-1.18	0.239	-1.44	0.151
Together	HW	Phyl Dist	-0.51	0.612	-0.32	0.749
Checkered	HW	Phyl Dist	0.79	0.430	0.12	0.907
Clumping	HW	EnvVar	0.57	0.571	1.58	0.114
Together	HW	EnvVar	**-2.20**	**0.027**	**-2.32**	**0.020**
Checkered	HW	EnvVar	-0.24	0.813	-0.73	0.465
Clumping	TreeS	Phyl Dist	**-2.24**	**0.025**	-0.42	0.678
Together	TreeS	Phyl Dist	-0.32	0.749	-0.69	0.488
Checkered	TreeS	Phyl Dist	1.24	0.214	0.04	0.966
Clumping	TreeS	EnvVar	-1.65	0.098	0.16	0.877
Together	TreeS	EnvVar	-1.22	0.222	-0.97	0.332
Checkered	TreeS	EnvVar	0.87	0.382	-0.18	0.854
Clumping	Diversity	Phyl Dist	-0.71	0.475	-0.09	0.932
Together	Diversity	Phyl Dist	-0.45	0.656	0.06	0.954
Checkered	Diversity	Phyl Dist	1.56	0.119	-1.51	0.131
Clumping	Diversity	EnvVar	-1.57	0.117	1.23	0.218
Together	Diversity	EnvVar	-0.40	0.689	-0.50	0.619
Checkered	Diversity	EnvVar	0.59	0.554	-0.07	0.947

Table 4.6.

Metric	Variable1	Variable2	Z-All	p-All	Z-Nearctic	p-Nearctic
Clumping	Species Occ.	Phyl Dist	-0.08	0.933	-0.98	0.327
Together	Species Occ.	Phyl Dist	0.44	0.663	0.75	0.454
Checkered	Species Occ.	Phyl Dist	-0.36	0.716	-0.65	0.516
Clumping	SM	Phyl Dist	-0.58	0.559	-1.36	0.173
Together	SM	Phyl Dist	-0.62	0.534	-0.27	0.784
Checkered	SM	Phyl Dist	-0.18	0.857	-1.69	0.092
Clumping	SM	EnvVar	1.02	0.310	1.12	0.263
Together	SM	EnvVar	-0.54	0.587	-0.55	0.584
Checkered	SM	EnvVar	-0.85	0.396	-0.82	0.411
Clumping	pH	Phyl Dist	1.49	0.137	0.19	0.852
Together	pH	Phyl Dist	1.58	0.114	0.83	0.405
Checkered	pH	Phyl Dist	-0.88	0.377	-0.10	0.918
Clumping	pH	EnvVar	-0.87	0.382	-0.95	0.341
Together	pH	EnvVar	0.24	0.814	0.01	0.995
Checkered	pH	EnvVar	0.20	0.845	0.10	0.917
Clumping	mLit	Phyl Dist	1.13	0.259	-0.65	0.517
Together	mLit	Phyl Dist	1.07	0.284	0.16	0.874
Checkered	mLit	Phyl Dist	1.21	0.227	0.70	0.487
Clumping	mLit	EnvVar	0.11	0.910	0.07	0.942
Together	mLit	EnvVar	-0.34	0.732	-0.65	0.515
Checkered	mLit	Phyl Dist	1.21	0.227	-1.03	0.302
Clumping	vLit	Phyl Dist	-1.18	0.239	-1.45	0.146
Together	vLit	Phyl Dist	-0.47	0.638	-0.21	0.834
Checkered	vLit	Phyl Dist	0.31	0.760	-0.85	0.396
Clumping	vLit	EnvVar	-0.46	0.643	-0.20	0.845
Together	vLit	EnvVar	1.03	0.301	0.75	0.454
Checkered	vLit	EnvVar	1.17	0.240	1.03	0.304
Clumping	SticksS	Phyl Dist	-0.61	0.544	0.95	0.343
Together	SticksS	Phyl Dist	-0.66	0.512	-0.07	0.944
Checkered	SticksS	Phyl Dist	0.16	0.873	-0.17	0.866
Clumping	SticksS	EnvVar	0.57	0.571	0.49	0.622
Together	SticksS	EnvVar	-0.72	0.473	-0.80	0.422
Checkered	SticksS	EnvVar	-0.49	0.625	-0.58	0.562
Clumping	SticksL	Phyl Dist	-0.91	0.363	0.04	0.968
Together	SticksL	Phyl Dist	-0.65	0.516	-0.85	0.394
Checkered	SticksL	Phyl Dist	0.77	0.440	0.79	0.428
Clumping	SticksL	EnvVar	0.59	0.554	0.37	0.711
Together	SticksL	EnvVar	-0.24	0.808	0.06	0.951
Checkered	SticksL	EnvVar	-0.25	0.802	0.07	0.941
Clumping	nSticks	Phyl Dist	0.16	0.871	-0.15	0.879
Together	nSticks	Phyl Dist	0.12	0.905	0.14	0.888
Checkered	nSticks	Phyl Dist	-0.58	0.563	-0.19	0.847
Clumping	nSticks	EnvVar	0.04	0.968	0.25	0.800
Together	nSticks	EnvVar	0.02	0.986	-0.03	0.973
Checkered	nSticks	EnvVar	0.49	0.624	0.53	0.595

Table 4.7.

R.C. Sample Code	LAT	LON	ALT	Shade	LitterD	%B	%L	%P	%S	%W	MAT	PDQ
APA_01	30.40317	-84.45607	33	18.6	25.0	4	76	20	0	0	19.4	263
APA_02	30.39119	-84.45990	30	24.4	7.0	20	16	64	0	0	19.6	266
APA_03	30.38031	-84.47223	38	16.0	24.3	0	8	92	0	0	19.6	266
APA_04	30.36093	-84.49108	35	24.4	58.5	0	4	96	0	0	19.6	266
APA_05	30.35131	-84.50819	35	11.2	33.3	0	68	32	0	0	19.6	266
APA_06	30.17619	-84.68185	5	14.1	27.3	0	64	36	0	0	19.8	266
APA_07	30.17687	-84.67563	4	14.4	30.3	20	8	72	0	0	19.8	266
APA_08	30.17655	-84.67837	6	10.6	27.0	0	76	24	0	0	19.8	266
APA_09	30.01125	-84.61632	5	9.0	24.0	8	28	32	0	32	19.9	263
APA_10	30.08155	-84.67151	11	33.1	31.3	0	68	32	0	0	19.8	267
BER_01	34.32553	-85.28114	386	11.4	21.5	8	68	8	16	0	15.1	278
BER_02	34.30241	-85.20329	209	10.1	45.5	0	96	4	0	0	15.4	272
BER_03	34.30077	-85.20484	196	12.9	8.3	60	20	20	0	0	15.4	272
BER_04	34.32282	-85.28743	526	3.0	37.5	0	76	16	8	0	15.1	278
BER_05	34.32327	-85.28569	478	38.4	9.3	40	16	32	12	0	15.1	278
BER_06	34.32253	-85.28670	475	11.1	28.3	0	56	36	8	0	15.1	278
BER_07	34.29911	-85.19979	182	18.4	20.0	20	4	76	0	0	15.4	272
BER_08	34.30084	-85.20188	204	8.4	31.5	4	92	4	0	0	15.4	272
BER_09	34.29782	-85.20566	199	4.8	23.0	4	76	20	0	0	15.4	272
BER_10	34.31580	-85.22607	211	12.2	34.0	0	84	16	0	0	15.3	274
BER_11	34.32181	-85.25566	236	48.7	16.3	4	16	68	12	0	15.1	278
BER_12	34.32902	-85.25010	356	11.8	41.8	0	96	0	4	0	15.1	278
BER_13	34.32797	-85.24973	324	4.5	30.3	12	52	32	4	0	15.3	274
BER_14	34.32983	-85.27505	364	10.5	26.5	0	60	4	36	0	15.1	278
BER_15	34.33128	-85.27205	358	11.2	44.8	0	52	12	36	0	15.1	278
BER_16	34.33042	-85.26257	305	2.5	34.5	4	52	36	0	8	15.1	278
BER_17	34.32377	-85.25210	270	4.9	24.8	0	96	4	0	0	15.1	278
BER_18	34.32548	-85.24751	279	3.5	17.5	8	84	4	4	0	15.3	274
BKR_01	30.86658	-86.93882	49	18.9	26.8	0	0	100	0	0	18.8	309
BLK_01	30.73244	-87.92242	12	6.5	31.0	0	96	4	0	0	19.4	314
BLK_02	30.73199	-87.92182	7	7.1	30.0	0	92	8	0	0	19.4	314
BLK_03	30.73186	-87.92118	3	4.1	51.3	0	52	24	0	24	19.4	314
BLK_04	30.73217	-87.91886	14	7.4	29.5	0	96	4	0	0	19.4	314
BLK_05	30.74564	-87.92538	2	2.9	17.3	0	68	20	0	12	19.4	314
BLK_06	30.74720	-87.92243	4	2.6	36.0	4	76	20	0	0	19.4	314
BLK_07	30.74686	-87.92275	6	4.3	47.8	0	28	72	0	0	19.4	314
BLK_08	30.74173	-87.92089	12	4.0	19.8	4	88	4	0	4	19.4	314
BLK_09	30.74183	-87.92035	17	4.6	33.0	0	88	12	0	0	19.4	314
BLK_10	30.74261	-87.92073	9	5.3	18.8	0	76	16	0	8	19.4	314
BLK_11	30.74721	-87.90823	22	15.6	16.0	12	0	88	0	0	19.4	317
BLK_12	30.73463	-87.91474	21	7.8	52.8	0	88	12	0	0	19.4	317
BUR_01	33.62124	-82.19067	59	5.9	20.3	8	72	20	0	0	16.8	227
BUR_02	33.62410	-82.19472	81	7.2	32.8	0	76	20	4	0	16.8	227

Table 4.7 continued

R.C. Sample Code	LAT	LON	ALT	Shade	LitterD	%B	%L	%P	%S	%W	MAT	PDQ
BUR_03	33.62269	-82.19719	79	50.6	16.8	0	24	48	28	0	16.8	227
BUR_04	33.62469	-82.19804	69	7.4	30.3	0	100	0	0	0	16.8	227
BUR_05	33.62173	-82.19518	70	10.2	37.8	0	40	56	4	0	16.8	227
BUR_06	33.62116	-82.23359	149	13.6	28.3	0	84	12	4	0	16.7	230
BUR_07	33.62370	-82.20219	120	9.3	53.3	0	60	8	32	0	16.8	227
CRK_01	30.84257	-81.54670	6	10.8	39.8	0	80	20	0	0	19.9	212
CRK_02	30.84215	-81.54363	4	17.4	30.3	0	48	52	0	0	19.9	212
CRK_03	30.84267	-81.54274	3	7.1	23.0	4	84	12	0	0	19.9	212
CRK_04	30.84328	-81.54192	2	9.1	28.3	0	84	16	0	0	19.9	212
CRK_05	30.84560	-81.54526	7	12.7	43.0	0	52	48	0	0	19.9	212
CRK_06	30.83845	-81.54998	6	16.7	22.8	4	32	64	0	0	19.9	212
CRK_07	30.83783	-81.55118	6	18.1	30.0	0	4	96	0	0	19.9	212
CRK_08	30.83904	-81.55882	4	7.7	56.8	0	52	48	0	0	19.9	212
CRK_09	30.83975	-81.55787	4	10.2	19.5	20	72	8	0	0	19.9	212
CRK_10	30.84047	-81.55736	4	8.5	20.5	4	80	8	0	8	19.9	212
CRK_11	30.84049	-81.56106	5	9.6	57.0	0	52	48	0	0	19.9	212
CRK_12	30.84297	-81.55934	5	7.9	32.5	4	84	12	0	0	19.9	212
CRK_13	30.84518	-81.55391	6	29.3	19.0	12	40	48	0	0	19.9	212
CRK_14	30.84436	-81.55442	6	11.9	56.3	0	80	20	0	0	19.9	212
CRK_15	30.84270	-81.55490	6	7.9	46.0	0	52	48	0	0	19.9	212
FDR_01	32.86436	-84.70256	346	9.8	35.5	0	52	16	32	0	16.4	258
FDR_02	32.86242	-84.70199	370	14.2	35.3	0	92	4	4	0	16.4	258
FDR_03	32.85776	-84.70446	366	8.1	18.3	8	52	32	0	8	16.4	258
FDR_04	32.85584	-84.70421	372	7.6	24.3	0	92	8	0	0	16.4	258
FDR_05	32.84067	-84.74563	423	9.8	33.3	0	56	4	40	0	16.4	258
FDR_06	32.84881	-84.81119	298	8.6	14.3	8	20	64	0	8	16.6	255
FDR_07	32.84866	-84.80988	309	7.9	34.3	0	88	12	0	0	16.6	255
FDR_08	32.85286	-84.81208	295	7.8	22.5	8	84	4	4	0	16.6	255
FDR_09	32.83989	-84.79120	317	6.2	30.3	4	92	4	0	0	16.5	257
FDR_10	32.83946	-84.79870	303	9.6	26.3	4	72	16	0	8	16.6	255
FDR_11	32.83984	-84.79916	307	6.4	39.8	0	88	4	8	0	16.6	255
FDR_12	32.83902	-84.82998	293	11.0	28.5	0	88	12	0	0	16.6	255
FDR_13	32.85254	-84.70389	385	11.8	43.8	0	92	8	0	0	16.4	258
FDR_14	32.84962	-84.70179	411	11.0	40.3	0	100	0	0	0	16.4	258
FDR_15	32.85218	-84.70482	385	4.5	21.3	8	60	24	8	0	16.4	258
GCF_01	31.52237	-82.77694	61	11.9	11.8	8	80	12	0	0	18.7	209
GCF_02	31.52151	-82.77474	67	31.4	14.5	48	20	16	16	0	18.7	209
GCF_03	31.51257	-82.75035	51	10.5	14.0	12	68	16	0	4	18.7	209
GCF_04	31.51224	-82.75110	50	13.8	42.0	0	80	20	0	0	18.7	209
GCF_05	31.51433	-82.74796	58	13.4	11.8	0	52	48	0	0	18.7	209
GCF_06	31.50903	-82.75733	63	11.8	25.3	0	80	16	4	0	18.7	209
GCF_07	31.51939	-82.76395	59	7.1	14.3	2	80	18	0	0	18.7	209
GRB_01	30.94341	-83.18883	60	7.6	19.0	10	70	20	0	0	19.4	185
GRB_02	30.94608	-83.19375	59	8.8	34.0	4	62	30	0	4	19.4	185
GRB_03	30.93902	-83.19564	61	55.1	17.8	16	6	78	0	0	19.4	185
GRB_04	30.93477	-83.18827	59	8.5	31.0	24	54	18	0	4	19.4	185

Table 4.7 continued

R.C. Sample Code	LAT	LON	ALT	Shade	LitterD	%B	%L	%P	%S	%W	MAT	PDQ
GRB_05	30.94020	-83.18367	58	93.9	18.3	6	36	58	0	0	19.4	185
HAN_01	32.11901	-84.74503	191	18.8	18.5	12	36	52	0	0	17.9	214
HAN_02	32.14046	-84.75383	104	14.7	14.8	10	68	22	0	0	18.1	209
HAN_03	32.15169	-84.75721	108	8.6	19.3	6	74	20	0	0	18.1	209
HAN_04	32.15183	-84.75648	106	8.7	37.8	0	88	12	0	0	18.1	209
HAN_05	32.15728	-84.75579	132	22.1	25.3	2	84	14	0	0	18.1	209
LWP_01	31.14287	-82.20769	32	12.8	45.3	0	74	26	0	0	19.3	215
LWP_02	31.14281	-82.20716	30	9.8	52.5	0	88	12	0	0	19.3	215
LWP_03	31.14196	-82.20704	28	5.6	44.8	2	64	10	0	24	19.3	215
LWP_04	31.14257	-82.21120	38	12.2	41.0	0	40	60	0	0	19.3	215
LWP_05	31.14293	-82.21101	38	18.9	13.3	14	16	70	0	0	19.3	215
LWP_06	31.14434	-82.20926	36	9.3	47.3	0	66	34	0	0	19.3	215
LWP_07	31.14257	-82.20969	36	12.3	45.0	0	32	68	0	0	19.3	215
LWP_08	31.14178	-82.20808	29	11.5	59.3	0	62	34	0	4	19.3	215
LWP_09	31.14301	-82.21008	36	10.5	34.5	4	60	28	0	8	19.3	215
LWP_10	31.13948	-82.21772	34	8.4	61.8	0	94	6	0	0	19.3	215
MDY_01	31.90884	-82.30679	41	15.2	23.8	0	28	72	0	0	18.8	203
MDY_02	31.90478	-82.31166	44	7.9	33.8	0	84	16	0	0	18.8	203
MDY_03	31.90685	-82.30855	47	9.5	13.8	6	14	80	0	0	18.8	203
MDY_04	31.90472	-82.31167	45	7.1	14.0	14	78	8	0	0	18.8	203
MDY_05	31.92718	-82.28278	66	18.3	15.5	12	20	68	0	0	18.9	203
MSP_01	32.87234	-81.96362	52	10.5	34.8	0	94	4	2	0	17.8	221
MSP_02	32.87242	-81.96280	53	11.9	34.5	0	84	16	0	0	17.8	221
MSP_03	32.87294	-81.96360	50	16.4	17.5	6	58	34	0	2	17.8	221
MSP_04	32.89110	-81.95239	56	11.9	17.3	0	98	2	0	0	17.7	223
MSP_05	32.88389	-81.95103	59	7.7	24.0	4	84	12	0	0	17.7	223
MZA_01	32.34163	-84.03160	82	6.4	22.5	0	6	14	80	0	18.0	202
MZA_02	32.33882	-84.02847	115	9.8	14.5	6	82	12	0	0	18.0	202
MZA_03	32.33861	-84.02944	98	4.4	22.5	2	94	4	0	0	18.0	202
OCA_01	29.22516	-81.65644	20	46.1	18.8	34	28	38	0	0	21.0	198
OCA_02	29.22540	-81.65367	17	49.9	8.0	34	22	44	0	0	21.0	198
OCA_03	29.26041	-81.68326	19	19.2	29.3	0	74	26	0	0	20.9	200
OCA_04	29.26524	-81.68876	15	14.1	38.3	0	60	40	0	0	20.9	200
OCA_05	29.25883	-81.68241	19	15.7	30.3	0	72	28	0	0	20.9	200
OCA_06	29.21230	-81.65466	2	11.5	46.8	4	70	20	0	6	21.0	198
OCA_07	29.24424	-81.64506	1	5.2	46.8	2	64	12	16	6	21.0	198
OCA_08	29.24418	-81.64505	1	3.5	34.8	0	70	30	0	0	21.0	198
OCA_09	29.27667	-81.68874	10	8.8	48.0	0	54	46	0	0	20.9	200
OCA_10	29.27540	-81.68853	10	10.8	41.3	0	62	2	0	36	20.9	200
OCA_11	29.08071	-81.57514	4	7.3	49.3	4	60	32	0	4	21.2	194
OCA_12	29.08147	-81.55882	10	19.7	39.0	0	72	28	0	0	21.2	194
OCA_13	29.14746	-81.83728	15	22.1	33.5	0	26	74	0	0	21.2	195
OCA_14	29.14743	-81.83622	16	31.5	44.3	0	54	46	0	0	21.2	195
OCA_15	29.14653	-81.83720	19	13.7	22.0	0	84	16	0	0	21.2	195
OCN_01	33.66570	-83.34339	192	10.8	20.0	2	18	80	0	0	18.1	237
OCN_02	33.67432	-83.33188	146	12.7	26.8	0	70	24	6	0	18.1	240

Table 4.7 continued

R.C. Sample Code	LAT	LON	ALT	Shade	LitterD	%B	%L	%P	%S	%W	MAT	PDQ
OCN_03	33.63725	-83.35034	159	7.4	25.5	0	98	2	0	0	18.1	237
OCN_04	33.63964	-83.34991	171	7.8	34.5	0	68	32	0	0	18.1	237
OCN_05	33.65869	-83.37477	139	5.3	17.0	2	74	24	0	0	18.1	237
OCN_06	33.65804	-83.37378	140	6.2	20.5	0	74	26	0	0	18.1	237
OCN_07	33.65774	-83.37445	139	7.7	26.5	4	86	10	0	0	18.1	237
OCN_08	33.66364	-83.36313	152	1.5	28.0	6	68	26	0	0	18.1	237
OCN_09	33.66332	-83.36292	150	6.9	16.0	6	80	10	0	4	18.1	237
OCN_10	33.66348	-83.35988	166	7.1	24.3	2	78	14	6	0	18.1	237
OCN_11	33.64533	-83.18965	175	5.9	30.0	2	94	4	0	0	17.9	238
OCN_12	33.64552	-83.18397	208	6.8	64.0	0	44	56	0	0	17.9	238
OCN_13	33.64901	-83.18091	170	3.8	27.0	0	54	44	0	2	17.9	238
OCN_14	33.65560	-83.18206	176	31.0	13.8	0	4	96	0	0	17.9	238
OCN_15	33.73475	-83.25900	156	5.7	26.8	6	66	28	0	0	18.0	242
OHP_01	32.57229	-82.45085	61	4.6	17.5	20	52	22	0	6	19.8	206
OHP_02	32.57070	-82.45145	67	15.7	28.8	4	72	24	0	0	19.8	206
OHP_03	32.56967	-82.45094	80	11.2	18.3	4	76	20	0	0	19.8	206
OHP_04	32.56933	-82.44987	82	20.1	21.3	22	44	34	0	0	19.8	206
OHP_05	32.56747	-82.45031	83	11.8	46.8	0	68	32	0	0	19.8	206
OKY_01	32.45934	-83.55987	130	12.2	35.8	0	36	64	0	0	19.7	206
OKY_02	32.44498	-83.52284	109	12.9	25.3	0	60	40	0	0	19.8	206
PIN_01	34.74338	-85.01558	477	8.6	63.5	2	86	6	6	0	15.8	298
PIN_02	34.73322	-85.01744	554	11.8	51.0	0	56	18	26	0	15.8	298
PIN_03	34.67662	-85.06569	302	3.9	23.0	6	46	44	0	4	15.5	301
PIN_04	34.62412	-85.02649	552	9.9	64.5	2	54	44	0	0	16.1	287
PIN_05	34.61346	-85.04617	271	3.7	23.0	10	68	22	0	0	15.9	291
PIN_06	34.61287	-85.08898	307	3.4	50.5	4	68	14	14	0	15.6	295
PIN_07	34.61281	-85.09207	337	5.2	38.5	2	64	10	24	0	15.6	295
PIN_08	34.60809	-85.07949	300	18.7	19.5	10	24	66	0	0	15.9	291
PIN_09	34.38935	-85.36146	298	6.3	37.5	0	68	8	24	0	16.2	281
PIN_10	34.56826	-85.24176	366	5.6	42.0	6	46	28	20	0	15.6	293
PIN_11	34.75211	-85.34839	294	3.1	46.3	0	36	64	0	0	16.0	287
PIN_12	34.65938	-85.38880	571	5.5	20.0	6	32	62	0	0	14.6	311
PIN_13	34.64896	-85.39127	567	15.3	24.5	4	32	14	50	0	14.6	311
PIN_14	34.65200	-85.38928	579	10.3	28.5	0	28	72	0	0	14.6	311
PIN_15	34.65707	-85.39032	592	9.9	29.3	0	74	24	2	0	14.6	311
PRC_01	32.06866	-84.91160	153	8.6	17.0	20	56	18	0	6	19.5	222
PRC_02	32.07006	-84.91209	182	7.0	12.5	58	22	16	2	2	19.5	222
PRC_03	32.06515	-84.91440	143	6.8	14.8	24	62	10	2	2	19.5	222
PRC_04	32.06827	-84.91381	192	4.1	25.8	6	76	14	4	0	19.5	222
RDH_01	31.73151	-87.38401	96	5.3	29.3	0	98	2	0	0	19.4	274
RDH_02	31.73392	-87.38123	87	16.1	24.8	18	42	18	16	6	19.4	274
RDH_03	31.73468	-87.38093	87	4.4	20.8	14	54	20	6	6	19.4	274
RDH_04	31.73122	-87.38553	95	8.8	31.3	4	76	14	6	0	19.4	274
RDH_05	31.73473	-87.38575	109	8.7	45.3	8	68	8	14	2	19.4	274
SCN_01	33.98879	-83.38415	189	4.2	20.5	0	88	12	0	0	17.6	265
SCN_02	33.98709	-83.38510	187	8.7	22.8	0	94	6	0	0	17.6	265

Table 4.7 continued

R.C. Sample Code	LAT	LON	ALT	Shade	LitterD	%B	%L	%P	%S	%W	MAT	PDQ
SCN_03	33.98635	-83.38370	190	4.7	19.0	0	90	8	2	0	17.6	265
SCN_04	33.98323	-83.38296	190	5.8	25.5	2	88	10	0	0	17.6	265
SCN_05	33.98326	-83.38277	194	7.3	27.8	2	78	16	4	0	17.6	265
SCN_06	33.98557	-83.38381	188	9.2	36.0	10	70	16	0	4	17.6	265
SCN_07	33.98488	-83.38158	196	13.5	26.5	0	84	14	2	0	17.6	265
SCN_08	33.98719	-83.37989	191	7.4	22.5	2	46	28	24	0	17.6	265
SCN_09	33.98854	-83.38119	202	3.5	39.3	0	90	10	0	0	17.6	265
SCN_10	33.98812	-83.38266	195	39.0	17.3	0	0	100	0	0	17.6	265
SCN_11	33.98896	-83.38339	193	3.4	19.3	2	82	16	0	0	17.6	265
SCN_12	33.98248	-83.38234	196	4.2	32.5	4	66	28	2	0	17.6	265
SCN_13	33.98124	-83.38010	187	42.3	16.8	0	0	100	0	0	17.6	265
SCN_14	33.98255	-83.38353	191	10.7	20.8	12	64	20	4	0	17.6	265
SCN_15	33.98931	-83.37937	191	7.5	29.8	0	94	6	0	0	17.6	265
SMN_01	30.80431	-84.86819	32	16.9	24.0	0	44	56	0	0	21.1	258
SMN_02	30.80178	-84.86544	33	12.7	36.0	0	76	22	0	2	21.1	258
SMN_03	30.80167	-84.86628	41	13.3	24.0	0	6	94	0	0	21.1	258
SMN_04	30.80280	-84.86524	29	12.4	28.3	0	78	18	0	4	21.1	258
SMN_05	30.80377	-84.86419	38	6.0	32.5	0	94	6	0	0	21.1	258
SMN_06	30.80300	-84.80685	26	12.8	24.8	26	16	58	0	0	21.1	256
SMN_07	30.80355	-84.80690	35	15.5	14.0	12	12	76	0	0	21.1	256
SMN_08	30.80368	-84.84742	30	11.5	40.5	0	88	12	0	0	21.1	258
SMN_09	30.80387	-84.84752	28	4.4	32.0	0	96	4	0	0	21.1	258
SMN_10	30.80418	-84.85087	36	9.6	42.8	0	80	0	20	0	21.1	258
SMN_11	30.83610	-84.85102	36	6.4	33.8	6	84	10	0	0	21.1	258
SMN_12	30.83685	-84.85165	33	8.6	18.5	2	86	10	0	2	21.1	258
SMN_13	30.83662	-84.85098	30	25.9	18.5	42	24	34	0	0	21.1	258
SMN_14	30.79918	-84.87605	27	12.9	25.0	4	10	86	0	0	21.1	258
SMN_15	30.80558	-84.86892	34	10.9	29.3	0	80	20	0	0	21.1	258
SPL_01	31.01779	-87.68672	61	17.8	4.3	26	6	66	0	2	20.4	320
SPL_02	31.01220	-87.69777	71	22.3	6.5	8	12	80	0	0	20.4	320
SPL_03	31.02235	-87.69334	76	22.0	7.5	10	14	76	0	0	20.4	320
SPL_04	31.01229	-87.68873	64	4.3	20.0	0	46	54	0	0	20.4	320
SRS_01	33.26838	-81.53863	66	16.9	31.0	4	66	26	0	4	19.0	221
SRS_02	33.34480	-81.49983	100	14.4	10.0	18	68	14	0	0	18.9	225
SRS_03	33.32977	-81.51647	94	12.2	49.8	0	24	76	0	0	18.9	224
SRS_04	33.37752	-81.59102	88	8.6	13.5	20	56	24	0	0	18.8	226
SRS_05	33.37499	-81.59402	91	17.4	42.0	34	22	44	0	0	18.8	226
SRS_06	33.37079	-81.62139	63	3.4	15.5	16	26	58	0	0	18.8	226
SRS_07	33.30750	-81.60644	94	14.6	18.0	6	88	6	0	0	18.8	223
SRS_08	33.31440	-81.66167	52	3.7	32.8	0	36	46	0	18	18.9	223
SRS_09	33.31785	-81.73783	94	3.2	50.8	0	94	6	0	0	18.7	225
SRS_10	33.31826	-81.73773	95	5.2	50.5	0	96	4	0	0	18.7	225
SRS_11	33.28593	-81.69499	38	2.5	28.8	0	78	22	0	0	18.9	223
SRS_12	33.26310	-81.72126	50	13.6	11.5	0	76	24	0	0	18.9	222
SRS_13	33.26309	-81.72071	49	38.7	47.5	6	0	94	0	0	18.9	222
SRS_14	33.26314	-81.71997	44	2.7	34.3	2	52	46	0	0	18.9	222

Table 4.7 continued

R.C. Sample Code	LAT	LON	ALT	Shade	LitterD	%B	%L	%P	%S	%W	MAT	PDQ
SRS_15	33.28457	-81.74375	57	7.5	70.0	0	98	2	0	0	18.9	222
SRS_16	33.29540	-81.51968	62	24.9	14.8	18	28	54	0	0	18.9	224
SRS_17	33.29540	-81.52057	65	31.0	11.3	38	30	32	0	0	18.9	224
SRS_18	33.29605	-81.52243	70	19.4	17.5	34	24	42	0	0	18.9	224
SRS_19	33.31286	-81.57211	89	12.6	24.8	2	80	18	0	0	18.9	224
SRS_20	33.32740	-81.58649	89	7.2	38.3	2	66	28	0	4	18.8	223
TAL_01	32.06822	-84.91371	190	4.2	33.8	10	52	10	26	2	19.5	222
TAL_02	34.73884	-83.39789	466	8.2	32.0	14	44	20	22	0	15.1	367
TAL_03	34.73882	-83.39194	408	4.9	63.3	2	50	8	40	0	15.1	367
TAL_04	34.74053	-83.39266	453	10.3	48.5	6	86	2	2	4	15.1	367
TAL_05	34.74085	-83.39448	477	4.1	39.0	0	96	2	2	0	15.1	367
TAL_06	34.73844	-83.38541	505	9.1	65.5	0	2	66	32	0	15.1	367
TAL_07	34.74148	-83.38631	492	8.1	50.8	0	78	20	2	0	15.1	367
TAL_08	34.73580	-83.38805	513	2.5	38.8	0	86	4	10	0	15.1	367
TAL_09	34.73623	-83.38880	468	6.5	44.5	0	82	14	4	0	15.1	367
TAL_10	34.74452	-83.39504	498	5.9	50.0	0	76	24	0	0	15.1	367
TAL_11	34.74040	-83.37805	495	36.9	7.0	26	12	46	16	0	15.1	367
TAL_12	34.73884	-83.37816	490	36.6	16.3	28	12	38	14	8	15.1	367
TAL_13	34.74128	-83.39464	481	8.8	22.3	2	46	44	8	0	15.1	367
TTR_01	30.64632	-84.25160	31	7.4	30.5	4	72	10	0	14	21.1	257
TTR_02	30.64986	-84.24899	33	6.6	34.3	2	54	44	0	0	21.2	256
TTR_03	30.65363	-84.25201	42	8.0	24.3	0	2	98	0	0	21.1	257
TTR_04	30.65598	-84.24580	42	4.0	21.0	6	48	46	0	0	21.2	256
TTR_05	30.66509	-84.25013	62	14.8	30.8	2	10	88	0	0	21.1	257
TTR_06	30.64260	-84.23160	31	12.3	25.5	6	72	22	0	0	21.2	256
TTR_07	30.65576	-84.23142	54	19.7	26.5	0	4	96	0	0	21.2	256
TTR_08	30.65906	-84.23329	50	10.5	45.8	0	86	14	0	0	21.2	256
TTR_09	30.65926	-84.23362	51	16.7	16.8	0	96	4	0	0	21.2	256
TTR_10	30.65914	-84.24432	44	5.2	34.5	0	80	20	0	0	21.2	256
TUG_01	34.49292	-83.06432	205	6.9	19.0	0	56	44	0	0	17.2	287
TUG_02	34.49431	-83.06709	219	3.8	25.0	0	80	16	4	0	17.2	287
TUG_03	34.49873	-83.06137	212	7.4	38.3	0	92	4	4	0	17.2	287
TUG_04	34.49515	-83.07097	215	31.7	15.5	6	0	92	2	0	17.2	287
TUG_05	34.49474	-83.06302	230	7.3	24.8	2	66	20	12	0	17.2	287
TWN_01	31.61646	-81.66640	25	7.7	58.5	0	82	18	0	0	21.1	208
TWN_02	31.59824	-81.67060	12	19.1	13.5	30	22	48	0	0	21.1	208
TWN_03	31.60263	-81.66947	12	8.0	29.0	0	90	10	0	0	21.1	208
TWN_04	31.59854	-81.66993	10	4.7	41.5	0	54	16	0	30	21.1	208
WDT_01	30.75970	-84.00042	72	20.0	10.0	4	0	96	0	0	21.2	248
WDT_02	30.76412	-84.00307	77	12.6	10.5	2	0	98	0	0	21.2	248
WDT_03	30.76115	-84.00752	64	11.3	10.0	0	12	88	0	0	21.2	248
WDT_04	30.75912	-84.00664	59	15.3	22.5	6	0	94	0	0	21.2	248
WDT_05	30.75914	-84.00091	69	11.3	23.0	2	80	12	0	6	21.2	248
WWF_01	35.03389	-83.01433	648	12.7	25.8	2	28	28	42	0	15.1	442
WWF_02	35.03247	-83.01490	695	4.3	19.3	6	44	18	24	8	14.6	442
WWF_03	35.03232	-83.01499	700	2.2	37.3	0	70	24	6	0	14.6	442

Table 4.7 continued

R.C. Sample Code	LAT	LON	ALT	Shade	LitterD	%B	%L	%P	%S	%W	MAT	PDQ
WWF_04	35.03012	-83.01490	746	9.3	48.5	2	74	18	6	0	14.6	442
WWF_05	35.02573	-83.01654	799	6.8	34.3	2	66	28	4	0	14.6	442
WWF_06	34.97533	-83.11615	622	7.4	40.8	0	38	60	2	0	15.1	436
WWF_07	34.96659	-83.10592	737	3.8	37.3	0	84	14	2	0	14.6	436
WWF_08	35.03321	-83.01781	864	13.4	23.8	40	14	26	20	0	15.6	442
WWF_09	34.96369	-83.07833	859	3.9	37.5	2	70	22	6	0	15.9	442
WWF_10	34.94312	-83.08591	688	6.1	43.8	0	98	0	2	0	16.0	442

Table 4.8.

Sample Code	S.abdita	S.angulata	S.apalachicolensis	S.boltoni	S.bunki	S.clypeata	S.creightoni	S.dietrichi	S.filirrhina	S.hyalina	S.laevinasis	S.metazytes	S.missouriensis	S.ohioensis	S.ornata	S.pergandei	S.pulchella	S.reflexa	S.rostrata	S.talpa	S.wrayi
APA01																				1	
APA02																					
APA03																					
APA04																					
APA05																					
APA06																					
APA07																					
APA08																					
APA09						1		1												1	
APA10																					
BER01															1		1				
BER02																					
BER03							1							1							
BER04															1						
BER05																					
BER06															1				1		
BER07																			1		
BER08																			1		
BER09															1				1		
BER10							1								1				1	1	
BER11																					
BER12																					
BER13															1						
BER14															1						
BER15										1									1		
BER16						1									1						
BER17															1				1		
BER18															1			1			
BKR01																					
BLK01																					
BLK02																					
BLK03																					
BLK04																					
BLK05																					
BLK06																					
BLK07		1																			
BLK08																					
BLK09																					
BLK10																					
BLK11																					
BLK12																					
BUR01																			1		
BUR02															1						
BUR03																					
BUR04																					
BUR05															1				1		
BUR06																			1		
BUR07															1						
CRK01								1												1	
CRK02																				1	
CRK03																					
CRK04																					
CRK05																					
CRK06																					
CRK07			1																		
CRK08																					
CRK09																					
CRK10		1																			

Sample Code	S.abdita	S.angulata	S.apalachicolensis	S.boltoni	S.bunki	S.clypeata	S.creightoni	S.dietrichi	S.filirrhina	S.hyalina	S.laevinasis	S.metazytes	S.missouriensis	S.ohioensis	S.ornata	S.pergandei	S.pulchella	S.reflexa	S.rostrata	S.talpa	S.wrayi
CRK11															1					1	
CRK12		1																			
CRK13																				1	
CRK14				1		1								1						1	
CRK15														1	1					1	
FDR01															1				1		
FDR02										1		1			1						
FDR03															1				1		
FDR04	1																		1		
FDR05																					
FDR06						1									1				1		
FDR07						1									1				1		
FDR08															1				1		
FDR09															1			1	1		
FDR10						1									1				1		
FDR11															1				1		1
FDR12															1				1		
FDR13											1				1				1		
FDR14															1	1			1		
FDR15															1	1			1		
GCF01																					
GCF02					1	1														1	
GCF03																			1		
GCF04																					
GCF05																				1	
GCF06						1															
GCF07																					
GRB01																				1	
GRB02														1	1					1	
GRB03																				1	
GRB04															1				1		
GRB05																					
HAN01																					
HAN02														1					1		
HAN03																			1		
HAN04																			1		
HAN05															1				1		
LWP01																					
LWP02																					
LWP03																					
LWP04																1					
LWP05																					
LWP06					1											1				1	
LWP07																1					
LWP08																			1		
LWP09																					
LWP10															1				1		
MDY01																					
MDY02																1				1	
MDY03																1				1	
MDY04																					
MDY05																					
MSP01															1						
MSP02															1				1		
MSP03					1					1				1	1				1		
MSP04															1						
MSP05					1										1						
MZA01														1	1				1		

Table 4.8 continued

Sample Code	S.abdita	S.angulata	S.apalachicolensis	S.boltoni	S.bunki	S.clypeata	S.creightoni	S.dietrichi	S.filirrhina	S.hyalina	S.laevinasis	S.metazytes	S.missouriensis	S.ohioensis	S.ornata	S.pergandei	S.pulchella	S.reflexa	S.rostrata	S.talpa	S.wrayi
MZA02														1					1		
MZA03								1						1	1				1		
OCA01																				1	
OCA02																					
OCA03																					
OCA04																					
OCA05																					
OCA06																					
OCA07																					
OCA08															1						
OCA09																				1	
OCA10																					
OCA11																					
OCA12																					
OCA13																					
OCA14																					
OCA15																					
OCN01						1									1				1		
OCN02														1	1	1			1		
OCN03						1								1	1				1		
OCN04																					
OCN05						1								1	1			1	1		
OCN06															1				1		
OCN07														1	1				1		
OCN08														1	1				1		
OCN09														1	1				1		
OCN10														1							
OCN11						1									1				1		
OCN12						1							1	1	1				1		
OCN13														1	1			1	1		
OCN14																					
OCN15															1				1		
OHP01																			1		
OHP02																					
OHP03						1															
OHP04															1						
OHP05																					
OKY01															1				1		1
OKY02							1							1	1						
PIN01																					
PIN02											1			1	1				1		
PIN03						1					1			1					1		
PIN04																			1		
PIN05						1					1			1						1	
PIN06											1				1						
PIN07		1									1				1						
PIN08															1					1	
PIN09															1						
PIN10						1		1						1	1				1		
PIN11																					
PIN12						1									1	1	1				
PIN13						1		1							1				1		
PIN14																		1			
PIN15	1														1						
PRC01															1				1		
PRC02						1									1				1		
PRC03																			1		
PRC04																					

Sample Code	S.abdita	S.angulata	S.apalachicolensis	S.boltoni	S.bunki	S.clypeata	S.creightoni	S.dietrichi	S.filirrhina	S.hyalina	S.laevinasis	S.metazytes	S.missouriensis	S.ohioensis	S.ornata	S.pergandei	S.pulchella	S.reflexa	S.rostrata	S.talpa	S.wrayi
RDH01												1							1		
RDH02																					
RDH03																			1		
RDH04																					
RDH05																					
SCN01														1	1			1	1		
SCN02							1							1	1				1		
SCN03														1	1				1	1	
SCN04														1				1			
SCN05									1					1	1	1			1	1	
SCN06							1							1	1		1	1	1		
SCN07														1	1			1			
SCN08														1	1						
SCN09														1	1				1	1	
SCN10																					
SCN11														1	1				1		
SCN12														1	1						
SCN13																					
SCN14														1	1		1	1	1	1	
SCN15							1								1				1		
SMN01															1					1	
SMN02															1					1	
SMN03															1						
SMN04															1						
SMN05															1						
SMN06															1						
SMN07								1												1	
SMN08															1						
SMN09															1						
SMN10															1						
SMN11															2					1	
SMN12															1						
SMN13															1						
SMN14																					
SMN15															1						
SPL01																			1		
SPL02															1						
SPL03																					
SPL04								1													
SRS01																					
SRS02								1													
SRS03															1						
SRS04							1														
SRS05																	1				
SRS06						1								1	1			1	1		
SRS07																					
OHP02																					
OHP03							1														
OHP04															1						
OHP05																					
OKY01															1				1		1
OKY02								1						1	1						
SRS08							1												1	1	
SRS09						1	1							1	1						
SRS10															1						
SRS11													1	1					1	1	
SRS12		1													1						
SRS13							1								1				1	1	

Table 4.8 continued

Sample Code	S.abdita	S.angulata	S.apalachicolensis	S.boltoni	S.bunki	S.clypeata	S.creightoni	S.dietrichi	S.filirrhina	S.hyalina	S.laevinasis	S.metazytes	S.missouriensis	S.ohioensis	S.ornata	S.pergandei	S.pulchella	S.reflexa	S.rostrata	S.talpa	S.wrayi
SRS14																					
SRS15			1		1								1							1	
SRS16															1						
SRS17							1								1						
SRS18			1																		
SRS19																					
SRS20															1						
TAL01																					
TAL02						1								1					1		
TAL03											1										
TAL04																			1		
TAL05															1				1		
TAL06																					
TAL07															1						
TAL08																					
TAL09														1							
TAL10															1						
TAL11															1						
TAL12																					
TAL13																					
TTR01																					
TTR02															1						
TTR03																					
TTR04																					
TTR05																					
TTR06																					1
TTR07																					

Sample Code	S.abdita	S.angulata	S.apalachicolensis	S.boltoni	S.bunki	S.clypeata	S.creightoni	S.dietrichi	S.filirrhina	S.hyalina	S.laevinasis	S.metazytes	S.missouriensis	S.ohioensis	S.ornata	S.pergandei	S.pulchella	S.reflexa	S.rostrata	S.talpa	S.wrayi
TTR08																					
TTR09																					
TTR10															1						
TUG01																					
TUG02																					
TUG03																					
TUG04																					
TUG05																					
TWN01																					
TWN02								1													
TWN03																					
TWN04																					
WDT01																					
WDT02																					
WDT03																					
WDT04																					
WDT05																					
WWF01														1	1				1		
WWF02														1					1		
WWF03							1							1	1				1	1	
WWF04							1		1					1	1					1	
WWF05							1					1		1	1						
WWF06							1							1					1		
WWF07							1							1	1						
WWF08							1							1	1	1				1	
WWF09							1							1	1	1			1	1	
WWF10							1							1	1				1	1	

Table 4.9.

L.C. Site	LAT	LON	ALT	MAT	PDQ	SM	mLit	vLit	StickS	StickL
FDR02M1	32.862369	-84.701296	375	16.4	258	21.0	28	0.17	6.2	3.5
FDR02M2	32.862229	-84.70243	358	16.4	258	17.4	32	0.16	5.6	2.4
FDR08M1	32.853143	-84.812469	293	16.6	255	19.6	32	0.18	3.1	2.4
FDR08M2	32.852956	-84.812814	287	16.6	255	19.2	19	0.14	4.4	2.4
FDR09M2	32.83969	-84.791248	316	16.5	257	18.8	27	0.17	3.8	2.4
FDR09M1	32.84002	-84.791495	319	16.5	257	28.8	35	0.17	3.9	3.8
FDR11M1	32.839627	-84.799167	310	16.6	255	17.2	55	0.18	4.1	1.3
FDR11M2	32.840392	-84.798978	317	16.6	255	79.2	33	0.18	6.8	3.7
FDR15M1	32.852228	-84.70486	386	16.4	258	12.7	26	0.31	5.2	3.2
FDR15M2	32.852067	-84.70486	386	16.4	258	12.0	22	0.14	6.4	2.4
MSP01M1	32.872722	-81.963131	53	17.8	221	17.8	19	0.12	6.4	3.2
MSP01M2	32.872567	-81.963378	53	17.8	221	34.0	40	0.16	3.9	2.6
MSP02M1	32.872537	-81.962549	52	17.8	221	19.8	44	0.17	2.5	2.0
MSP02M2	32.872605	-81.96288	47	17.8	221	14.2	45	0.20	2.3	1.8
MSP03M1	32.873045	-81.96347	52	17.8	221	37.0	18	0.10	5.9	1.9
MSP03M2	32.872926	-81.96368	55	17.8	221	38.4	19	0.15	5.8	1.5
MSP04M2	32.890893	-81.952871	59	17.7	223	53.8	27	0.13	4.1	1.9
MSP04M1	32.890866	-81.953028	72	17.7	223	60.8	27	0.15	5.6	2.8
MSP06M1	32.878996	-81.957497	57	17.7	223	67.5	21	0.12	7.8	1.6
MSP06M2	32.879282	-81.957628	57	17.7	223	24.2	26	0.13	6.2	3.4
OCN12M1	33.645497	-83.184008	205	16.5	238	54.2	67	0.31	3.2	2.5
OCN12M2	33.645697	-83.184027	206	16.5	238	48.0	59	0.22	2.9	2.6
PIN05M1	34.612749	-85.046489	270	14.6	291	40.6	46	0.26	2.2	2.1
PIN05M2	34.613534	-85.04617	269	14.6	291	61.2	34	0.30	4.5	1.8
PIN10M1	34.574826	-85.23458	322	14.4	293	35.8	37	0.24	5.5	1.8
PIN10M2	34.574053	-85.235939	324	14.4	293	36.6	29	0.22	5.9	2.6
PIN12M1	34.65938	-85.38881	570	13.5	311	51.2	20	0.15	3.4	1.2
PIN12M2	34.659148	-85.388609	571	13.5	311	19.0	26	0.16	7.5	2.5
PIN15M1	34.65707	-85.39032	591	13.5	311	10.0	35	0.24	5.1	2.4
PIN15M2	34.657032	-85.390506	592	13.5	311	19.6	32	0.21	5.7	1.5
SCN05M1	33.98326	-83.38277	219	16.2	265	32.2	55	0.22	3.4	3.3
SCN05M2	33.984164	-83.382242	221	16.2	265	17.5	34	0.18	8.0	4.4
SCN06M1	33.984926	-83.381455	226	16.2	265	28.0	32	0.15	7.7	2.3
SCN06M2	33.984642	-83.381543	227	16.2	265	24.3	35	0.18	7.6	3.1
SCN59M1	33.98944	-83.38038	210	16.2	265	51.6	17	0.12	6.8	3.6
SCN59M2	33.989504	-83.380326	207	16.2	265	62.6	4	0.08	2.3	2.2
SRS04M1	33.377593	-81.591205	91	17.3	226	18.0	25	0.11	4.6	2.2
SRS04M2	33.377872	-81.590958	92	17.3	226	15.2	18	0.12	4.1	1.8
SRS11M1	33.28657	-81.695061	48	17.4	223	45.2	20	0.13	7.0	3.1
SRS11M2	33.284836	-81.695892	45	17.4	223	52.0	33	0.15	6.5	3.4
SRS12M1	33.263	-81.72126	60	17.4	222	20.2	16	0.13	8.1	2.9
SRS12M2	33.26301	-81.721409	62	17.4	222	18.6	35	0.16	7.7	2.6
SRS15M1	33.284402	-81.743478	67	17.4	222	14.0	62	0.16	0.3	1.9
SRS15M2	33.284914	-81.743485	70	17.4	222	14.6	59	0.19	0.0	2.1
SRS20M1	33.33342	-81.607218	58	17.3	226	23.0	36	0.15	5.7	3.0
SRS20M2	33.334342	-81.608022	59	17.3	226	28.8	30	0.14	8.8	4.4

Table 4.9 continued

L.C. Site	nTrees	DBH	HW	TreeS	TreeDiv
FDR02M1	13	61.8	1.00	3	1.22
FDR02M2	12	66.8	1.00	3	1.28
FDR08M1	15	85.9	0.67	5	2.63
FDR08M2	11	87.1	0.91	8	13.19
FDR09M2	13	88.8	0.85	5	2.98
FDR09M1	12	84.5	0.83	3	1.28
FDR11M1	12	77.1	0.44	5	2.53
FDR11M2	6	109.3	1.00	4	5.25
MSP01M1	3	125.3	0.67	2	3.17
MSP01M2	5	216.8	0.80	4	9.28
MSP02M1	7	86.9	0.11	2	0.64
MSP02M2	9	95.7	0.00	1	0.29
MSP04M2	16	53.3	0.88	5	2.60
MSP04M1	6	85.3	0.83	5	14.12
MSP06M1	11	93.5	1.00	5	3.58
MSP06M2	14	95.3	0.93	6	3.99
OCN12M1	16	100.7	0.06	2	0.61
OCN12M2	28	85.1	0.14	3	1.61
PIN05M1	8	104.6	0.88	6	10.91
PIN05M2	12	96.3	1.00	5	3.22
PIN10M1	11	98.1	0.73	7	8.29
PIN10M2	9	108.9	1.00	7	26.78
PIN12M1	10	67.4	1.00	5	3.98
PIN12M2	11	81.5	1.00	8	13.19
PIN15M1	18	72.4	1.00	2	0.61
PIN15M2	15	69.1	1.00	5	2.63
SCN05M2	7	112.0	1.00	4	3.88
SCN06M1	8	104.9	1.00	4	3.18
SCN06M2	11	83.5	1.00	5	3.54
SRS04M1	19	56.4	0.95	4	1.67
SRS04M2	23	45.7	0.96	5	2.07
SRS11M1	12	64.5	1.00	6	5.40
SRS11M2	12	98.7	1.00	7	8.29
SRS12M1	29	46.7	1.00	2	0.49
SRS12M2	34	43.2	0.85	4	1.18
SRS15M1	7	103.1	0.00	1	0.32
SRS15M2	15	93.4	0.00	1	0.25
SRS20M1	15	85.1	0.93	7	5.11
SRS20M2	22	82.3	1.00	9	6.02

Table 4.9 continued

L.C. Site	Clay	Loose	Rocky	Sand	Humus	Branch	Rock	Dep.	Log	Open	Stump
FDR02M1	0.00	1.00	0.92	0.96	0.96	0.48	0.20	0.12	0.00	0.16	0.04
FDR02M2	0.00	0.92	0.40	0.72	1.00	0.32	0.00	0.16	0.16	0.24	0.08
FDR08M1	0.84	0.28	0.00	0.84	0.28	0.24	0.08	0.08	0.08	0.56	0.00
FDR08M2	1.00	0.12	0.00	1.00	0.12	0.20	0.00	0.12	0.04	0.48	0.08
FDR09M2	0.84	0.52	0.72	0.84	0.52	0.28	0.36	0.00	0.08	0.32	0.04
FDR09M1	0.72	0.56	0.04	0.72	0.56	0.28	0.00	0.04	0.04	0.28	0.04
FDR11M1	0.72	0.96	0.08	0.92	0.96	0.00	0.00	0.16	0.12	0.36	0.04
FDR11M2	0.00	1.00	0.00	0.00	1.00	0.24	0.00	0.04	0.08	0.52	0.00
FDR15M1	0.00	0.88	0.84	0.36	0.72	0.24	0.48	0.16	0.00	0.20	0.04
FDR15M2	0.00	0.16	0.00	0.84	1.00	0.24	0.00	0.16	0.00	0.68	0.00
MSP01M1	0.00	0.56	0.00	0.96	0.88	0.40	0.00	0.00	0.08	0.40	0.00
MSP01M2	0.00	0.84	0.00	1.00	1.00	0.32	0.00	0.00	0.16	0.28	0.00
MSP02M1	0.00	0.64	0.00	0.96	0.96	0.48	0.00	0.16	0.12	0.04	0.08
MSP02M2	0.00	0.76	0.00	0.96	0.96	0.36	0.00	0.00	0.08	0.24	0.12
MSP03M1	0.00	0.76	0.00	0.88	0.68	0.12	0.00	0.16	0.16	0.48	0.00
MSP03M2	0.00	0.56	0.00	1.00	1.00	0.04	0.00	0.08	0.00	0.68	0.00
MSP04M2	0.00	0.52	0.00	0.76	0.96	0.24	0.00	0.24	0.00	0.24	0.00
MSP04M1	0.00	0.48	0.00	0.64	1.00	0.08	0.00	0.04	0.00	0.32	0.16
MSP06M1	0.00	0.08	0.00	1.00	1.00	0.16	0.00	0.04	0.00	0.44	0.00
MSP06M2	0.00	0.20	0.00	1.00	1.00	0.40	0.00	0.04	0.04	0.44	0.00
OCN12M1	0.96	1.00	0.00	0.00	1.00	0.36	0.00	0.04	0.04	0.52	0.00
OCN12M2	1.00	1.00	0.00	0.00	1.00	0.24	0.00	0.00	0.16	0.40	0.04
PIN05M2	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.04	0.42	0.00
PIN10M1	0.44	0.72	0.44	0.60	0.28	0.04	0.00	0.08	0.32	0.28	0.04
PIN10M2	0.56	0.52	0.00	0.64	0.48	0.24	0.04	0.04	0.20	0.28	0.00
PIN12M1	0.00	0.20	0.00	0.00	0.16	0.08	0.00	0.00	0.04	0.64	0.12
PIN12M2	0.00	0.04	0.00	0.92	0.04	0.16	0.00	0.16	0.00	0.60	0.00
PIN15M1	0.00	0.92	0.52	0.88	0.00	0.24	0.08	0.08	0.00	0.52	0.00
PIN15M2	0.20	0.60	0.08	0.76	0.28	0.20	0.00	0.00	0.20	0.44	0.00
SCN05M1	0.04	0.92	0.04	0.00	0.92	0.12	0.00	0.04	0.12	0.40	0.04
SCN05M2	0.00	1.00	0.00	0.00	1.00	0.44	0.00	0.20	0.00	0.36	0.04
SCN06M1	0.68	0.72	0.00	0.00	0.76	0.20	0.04	0.16	0.16	0.40	0.08
SCN06M2	0.36	1.00	0.44	0.08	1.00	0.28	0.28	0.16	0.08	0.28	0.00
SCN59M1	1.00	0.20	0.04	0.00	0.12	0.28	0.00	0.00	0.00	0.40	0.00
SCN59M2	1.00	0.00	0.00	0.00	0.00	0.36	0.08	0.00	0.08	0.44	0.00
SRS04M1	0.00	0.92	0.00	0.60	0.88	0.12	0.00	0.08	0.00	0.36	0.04
SRS04M2	0.00	0.92	0.00	0.96	0.76	0.20	0.00	0.08	0.00	0.44	0.00
SRS11M1	0.00	0.96	0.00	0.00	1.00	0.20	0.00	0.12	0.00	0.36	0.00
SRS11M2	0.00	0.84	0.00	0.00	1.00	0.16	0.00	0.12	0.32	0.24	0.08
SRS12M1	0.00	0.60	0.00	0.76	0.88	0.40	0.00	0.04	0.04	0.36	0.04
SRS12M2	0.00	0.76	0.00	1.00	0.96	0.24	0.00	0.16	0.00	0.40	0.04
SRS15M1	0.00	1.00	0.00	1.00	1.00	0.24	0.00	0.00	0.08	0.44	0.00
SRS15M2	0.00	0.68	0.00	1.00	1.00	0.08	0.00	0.00	0.00	0.68	0.00
SRS20M1	0.00	0.56	0.00	0.12	1.00	0.24	0.00	0.20	0.04	0.32	0.00
SRS20M2	0.00	0.48	0.00	0.80	1.00	0.16	0.00	0.20	0.00	0.44	0.04

Table 4.10.

Sample Code	S.apalachicolensis	S.bunki	S.carolinensis	S.clypeata	S.creightoni	S.dietrichi	S.filirrhina	S.hyalina	S.laevinasis	S.metazytes	S.missouriensis	S.ohioensis	S.ornata	S.pergandei	S.pilinasis	S.pulchella	S.reflexa	S.rostrata	S.talpa
FDR02M1																		1	
FDR02M2																			
FDR08M1			1										14					1	1
FDR08M2													14						1
FDR09M1													7					6	
FDR09M2													9					5	
FDR11M1													10					1	
FDR11M2													8					14	
FDR15M1													6						
FDR15M2													4	1				1	
MSP01M1		1			1							1	5					2	
MSP01M2					1								5						2
MSP02M1							1					1		2	1		1	6	
MSP02M2															3	1		3	
MSP03M1												1	3		1				
MSP03M2		3			1	1						7	5			2			4
MSP04M1					1			1					1					1	
MSP04M2																		3	
MSP06M1													12					2	
MSP06M2								1			1		7						
OCN12M1												2					1	6	
OCN12M2																		6	
PIN05M1							2		5			11							2
PIN05M2				2					2			4	3						
PIN10M1				4		1			2				4						2
PIN10M2				1									4					5	
PIN12M1				1									6	1					
PIN12M2													9						
PIN15M1										1			2						
PIN15M2				1						1			2						
SCN05M1												7	2			2			
SCN05M2									1			12						1	
SCN06M1												3	2						
SCN06M2							1					2	3						1
SCN59M1				1					1			20	10				1	8	3
SCN59M2					1				1			14						12	1
SRS04M1					2								2						
SRS04M2													1						
SRS11M1											1	8	5		1			21	1
SRS11M2																		1	2
SRS12M1					2								8					1	1
SRS12M2													1					3	6
SRS15M1	2	7											5						
SRS15M2		7			3						1		1					1	
SRS20M1				1									1					7	
SRS20M2				1									3					2	

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