CLASSIFICATION OF SMALL-MAMMAL METACOMMUNITY STRUCTURES

ALONG ELEVATIONAL GRADIENTS WITH CONNECTIONS TO

METACOMMUNITY NETWORKS

by

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DEDICATION

To my loving, supportive, nerdy parents, Kathryn Amacher and Robert Javan.

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LIST OF ABBREVIATIONS

Abbreviation

Description

- EMS Elements of Metacommunity Structure
- HC3 Heteroscedasticity Consistent Covariance Matrix 3
- IUCN International Union for Conservation of Nature
- MC Metacommunity
- MCS Metacommunity Structure
- NODF_{max} Maximum Nestedness Metric Based on Overlap and Decreasing Fill
- N_{rel} Relativized Nestedness
- OLS Ordinary Least Squares
- SDR Species Deletion Ratio
- SG Spinglass Algorithm
- LV Louvain Method

ABSTRACT

Small-mammals respond quickly to habitat changes and serve an important role in ecosystem function as prey and sources of seed dispersal. To assess the interaction structure, or metacommunity structure, of small-mammal assemblages, I collected presence-absence surveys of non-volant, terrestrial mammals weighing less than nine kilograms along elevational gradients from the literature at local and regional scales. In total, fifty-nine sources were used to delimit 337 species incidence matrices from 104 study sites and six taxonomic groups. Small-mammal metacommunity structures were predominantly quasi-anti-nested and anti-nested, but could differ depending on taxonomic group. Elevational gradients were highly correlated with the latent environmental gradient, implying anti-nested small-mammal metacommunity structures were likely the result of species-specific responses to changes in the elevational gradient. Random metacommunity structures generally reflected disconnected metacommunity networks. Metacommunity networks treat species as nodes with connecting edges weighted by species co-occurrence at elevational bands. Metacommunity structure and additional nestedness metrics I calculated did not depend on maximum elevation, average annual mean temperature, average annual precipitation, or the number of species clusters in the network. Relativized nestedness was the only nestedness metric that increased as the species deletion ratio (a measure of network connectivity) increased, demonstrating highly nested metacommunities were also highly connected.

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1. INTRODUCTION

The study of species distributions over environmental gradients has a long history in ecology and important insights have been derived from the examination of patterns with respect to biotic change (Clements 1904; Diamond 1975; Wiens and Donoghue 2004). Nested patterns of species assemblages can be caused by wide variety of factors, including habitat heterogeneity (Wang et al. 2010), passive sampling (Cutler 1994), and selective species extinctions and colonizations (Herczeg and Horvath 2015). Elevational gradients occur globally, host a wide variety of species, and exhibit high habitat heterogeneity, thus are an ideal environmental gradient to detect nestedness patterns. An elevational gradient is also uniquely suited to understanding ecological mechanisms such as population processes and species interactions, because changes in elevation are correlated with abiotic and biotic changes (Willig et al. 2011). The intensity of habitat and community composition change will depend on the topographic gradient of the region as well as its geographic location (Whittaker 1967). Species within tropical climates or distributed across large distances may experience marked changes in habitat as elevation increases compared with those in temperate climates or assessed over shorter distances (Barone et al. 2008). In other words, relatively homogenous, low-energy systems likely exhibit nested patterns, while heterogeneous, high-energy systems likely exhibit anti-nested patterns (Henriques-Silva, Lindo, and Peres-Neto 2013).

The elements of metacommunity structure (EMS) framework provides an analytical approach to assess the metacommunity structure, i.e. nested and anti-nested patterns, of species assemblages along an underlying or latent environmental gradient (Leibold and Mikkelson 2002; Presley, Higgins, and Willig 2010). A metacommunity is a

set of communities linked through the dispersal of their constituent species (Leibold et al. 2004). The EMS framework is often applied to sets of islands (Presley and Willig 2010) and lakes (Henriques-Silva, Lindo, and Peres-Neto 2013), but can also be applied to elevational gradients (Lopez-Gonzalez and Lozano 2015). Small-mammals are an ideal taxonomy for investigating nestedness patterns along elevational gradients, because they respond quickly to habitat changes and play a significant role in ecosystem function by influencing forest succession through seed predation and dispersal, as well as by being prey (Pardini et al. 2005).

Three EMS (coherence, turnover, and boundary clumping) combine to create three broad classifications of metacommunity structure (random, nested, and anti-nested) (Leibold and Mikkelson 2002). A perfectly coherent metacommunity has no gaps or embedded absences in a species distribution along the latent gradient (Leibold and Mikkelson 2002). Turnover quantifies the number of times one species replaces another along the gradient. Boundary clumping occurs when only specific sets of species coincide with each other due to environmental filtering, such as changes in habitat, competitive exclusion, or predation. When metacommunity mechanisms are governed primarily by stochastic processes, a random metacommunity structure will arise in which species spatial distributions are no different than distributions produced by chance. Analytically, a random metacommunity structure lacks significant coherence. Nested metacommunity structure results when the distributions of some species along the environmental gradient wholly reside within the distribution of others. This is analytically indicated by positive coherence and negative species turnover (Leibold and Mikkelson 2002). Anti-nested metacommunity structures result from negative coherence alone (i.e. checkerboard

structure) or positive coherence and positive turnover (Leibold and Mikkelson 2002).

Another way to view a metacommunity is as a network of species co-occurrence. A metacommunity network is a representation of species (nodes) connected by their cooccurrence (edges) along a gradient (Figure 1). The relationship between the connectedness of metacommunity networks and the nestedness of metacommunity assemblages has been explored (Fortuna et al. 2010), as well as the validity of turnover as a nestedness metric (Gotelli and Ulrich 2012; Schmera et al. 2018). Yet, direct analysis of the relationship between metacommunity structure as defined by the EMS framework and metacommunity networks is still lacking. A nestedness metric based on the connectivity of a network may be able to bridge the gap between turnover (species replacements) and metacommunity networks.

One goal of my research was to test the validity of a nestedness metric I defined, the species deletion ratio (SDR), in distinguishing between anti-nested and nested metacommunities based on network connectivity. To achieve this goal, I focused on assemblages of non-volant, terrestrial mammals weighing less than nine kilograms grouped by taxonomy along elevational gradients at local and regional scales. In addition to nestedness as defined by the EMS framework (turnover) and my nestedness metric (SDR), I assessed two gradient independent measures of nestedness, relativized nestedness (N_{rel}) and maximum nestedness metric based on overlap and decreasing/differing fill (NODF_{max}). I investigated other possible influences on metacommunity structures, such as matrix size, and three abiotic factors on all nestedness metrics (maximum elevation, temperature, and precipitation). Finally, two clustering algorithms, the Louvain method and Spinglass algorithm, were used to detect the number

of species clusters within a metacommunity network.

Hypotheses

- Sites with a high maximum elevation likely have high species turnover, due to increased habitat heterogeneity, resulting in anti-nested metacommunity structures (high turnover) and low nestedness metrics (N_{rel}, NODF_{max}, and SDR).
- 2. Small-mammals are sensitive to changes in evaporation and temperature, therefore precipitation and temperature may be limiting factors to small-mammal species distributions along elevational gradients. As a result, small-mammal metacommunities will increase in nestedness as temperature and precipitation increase.
- 3. SDR will reflect the difference between nested and anti-nested metacommunities, therefore turnover will decrease with as SDR increases. Nestedness metrics independent of a latent environmental gradient (N_{rel}, and NODF_{max}) will increase as SDR increases.
- A greater number of species clusters will produce anti-nested metacommunities, consequently nestedness will decrease in magnitude as the number of identified species clusters increases.

2. METHODS

Data Collection

Incidence matrices were obtained from peer-reviewed journal articles and books in which non-volant terrestrial mammals nine kilograms or under, referred to as smallmammals, were reported along an elevational gradient. Keywords searched on the Texas State Library website and Google Scholar included "small mammal", "elevational gradient", "altitudinal gradient", "mammal survey", and the names of well-known mountains or mountain ranges. Each data set was organized into an elevation (row) by species (column) incidence matrix. If species *i* was found at elevation *i*, then it received a one in cell (i, j) and zero otherwise. All incidence matrices required a minimum of six elevational bands and eight species to be included in analyses. All species within an incidence matrix were assumed to have a continuous spatial distribution along the elevational gradient. The maximum number of elevational bands was determined by taking the difference between the highest and lowest elevation of all species in the assemblage, then dividing this range into 100 meter intervals, starting with the lower bound rounded to the tens place. Using 100 meters as the width of elevational bands was an arbitrary choice, but as a result the minimum elevational range that could be used was 600 meters long. A continuous elevational distribution was assumed to wave restrictions on trapping effort between elevational bands. Incidence matrices were generated in R version 3.4.0 (R Core Team 2017) with a function that took in a list of species and their corresponding minimum and maximum elevational distribution then populated a matrix of zeros with ones to indicate a species' presence. Any elevational bands that remained empty (row sum of zero) after the matrix was populated were removed. Therefore, the

number of elevational bands (incidence matrix rows) may be less than the maximum number of 100 meter elevational bands along the sampled gradient.

Each incidence matrix was classified by the scale, local or regional, at which species were sampled along the elevational gradient. Local-level incidence matrices consisted of species sampled along a single elevational transect during one or more seasons, but not exceeding a five-year survey period. Species were counted as present in an elevational band if they were caught, seen, or species-specific burrows were found at a location. Animal tracks, remains or droppings were not considered sufficient evidence of a species' presence. Species' elevational distributions contained in all local-level incidence matrices come from one source of information and represented individual transects without overlapping areas. Regional-level incidence matrices consisted of species elevational distributions reported for more than a five-year period, across multiple elevational transects or included information from trapping records, museum specimens, and field notes (McCain 2005). Regional-level matrices were created from one source or multiple local-level matrices combined. At both scales, study site refers to a surveyed region that does not share any overlapping area with other locations at that scale. Multiple regional-level incidence matrices were not combined to ensure there was no overlapping area between study sites at the regional-level. Local-level incidence matrices represented a snapshot in time, because they only depended on species elevational distributions from a short time-frame. Regional-level incidence matrices, on the other hand, may have relied on historical records of species elevational distributions to create a report of species known to exist in the region. As a result, local and regional matrices were analyzed separately.

All species classifications were aligned to the same taxonomic reference (Wilson and Reeder 2005). Species described after 2005 cannot be found in the taxonomic reference, but are acknowledged on the IUCN Red List (IUCN 2018). Superorders were based on the most recent published phylogeny for therian mammal orders that included only monophyletic orders (Foley, Springer, and Teeling 2016). Mammal assemblages were compiled for each study site by the taxonomic relatedness of species. The six possible taxonomic groupings were genus, family, suborder, order, superorder, and multiple superorders. An assemblage was created if at least eight species belonged to a taxonomic relatedness group. For example, if eight species in the genus Akodon were reported at a study site then an incidence matrix was created with only those species. If instead seven species were in the genus Akodon and one in the genus Peromyscus, then an incidence matrix was created but classified as having the same family, Cricetidae. Assemblages within a study site are not independent because they share overlapping sampled area, but assemblages are independent between study sites and within a taxonomic group.

Site-specific information included maximum elevation of the surveyed area, average annual mean temperature, and average annual precipitation. Maximum elevation is not the highest point surveyed, but the highest peak in the surveyed region. When this information was not cited in-text, it was assessed using Google Maps relief view (Google 2018). Average annual mean temperature and average annual precipitation were determined for each study site based on 1960-1990 data provided in WorldClim version 1 (Hijmans et al. 2005). The term average annual mean temperature may sound redundant, but I use it to emphasize the value is an average for each study site based on the annual

mean temperature from 1960-1990. Annual mean temperature represented an average of the daily high and low temperatures for each day. Data were accessed with version 2.5-8 of the "raster" package in R using the function "getData" for the Worldclim biological variables at a finest available resolution of 30 arc-seconds (Hijmans 2016). All smallmammal assemblages created for a single study site (i.e. incidence matrices of different taxonomic groups within that site) have identical values for maximum elevation, average annual mean temperature, and average annual precipitation.

Metacommunity Structure

Each incidence matrix was ordinated along the first axis of correspondence via reciprocal averaging to minimize the number of embedded absences (Gauch, Whittaker, and Wentworth 1977). To determine if the underlying gradient (latent environmental gradient) was correlated with the elevational gradient, I computed the Spearman rank correlation (ρ) between component scores of each elevational band and elevation in meters (Willig et al. 2011). The elevational and latent environmental gradient were considered highly correlated for the absolute value of $\rho \ge 0.8$, i.e. either a strong positive or negative correlation. Elevational band component scores were calculated in R with the function "OrderMatrix" in the package "metacom" version 1.5.0 (Dallas 2018), then correlation was determined with the function "cor" and method set to "spearman".

All incidence matrices were analyzed in MATLAB version R2018a with the "EMS" library using the function "metacommunity" ("MATLAB and Statistics Toolbox" 2018; Higgins 2005). I determined coherence and turnover for each incidence matrix by applying a Monte Carlo-like algorithm to generate a null distribution (Harrison 2010). To test if an incidence matrix had significant positive or negative coherence, the number of

embedded absences were counted for the input matrix after transformation via reciprocal averaging. Next, 1000 random matrices of the same rank were generated and ordinated by reciprocal averaging, then each of their respective embedded absences counted. Species richness (the row sum) was conserved per elevational band and species occurrence at an elevation was proportional to the input incidence matrix (variable column sums). The number of ones and zeros allowed in the random incidence matrices can differ based on the null model used to generate them. Ideally, a moderate null model balances type I and type II error, i.e. one not too conservative or too liberal (Gotelli 2000). The most liberal null model choice does not restrict row or column sums as long as no row or column contains only zeros (Leibold and Mikkelson 2002). The most conservative null models require row and column sums of random matrices to be the same as those of the input incidence matrix. After determining the number of embedded absences across all random incidence matrices, each value was fit to a z-distribution, thereafter an empirical p-value was computed based on the z-score of the original incidence matrix. The same process was done to test the significance of turnover, except by calculating the number of species replacements along the gradient and then normalizing.

Random and non-random metacommunity structures were distinguished by whether the observed number of embedded absences (coherence) was significant (p < 0.05). If the number of embedded absences was significantly greater than expected due to random chance (negative coherence), then the incidence matrix was classified as having checkerboard metacommunity structure (Diamond 1975). Metacommunity structures with significant positive coherence were divided into four categories, nested, quasi-

nested, quasi-anti-nested, and anti-nested. Nested metacommunity structures had significantly (p < 0.05) fewer species replacements (less turnover) than expected due to random chance, while anti-nested structures had significantly more. If turnover was not significant, then the resulting metacommunity structure was considered quasi-nested or quasi-anti-nested (Presley, Higgins, and Willig 2010). An incidence matrix had quasinested structure if the observed number of species replacements was less than the mean, but quasi-anti-nested if it was greater than the mean.

The number of embedded absences may be impacted by the number of elevational bands (rows), while the number of species replacements may increase with the number of species (columns). P-values for coherence were predicted by the number of elevational bands and turnover p-values by the number of species within in an incidence matrix. A robust linear regression was modeled for each taxonomic group with at least ten incidence matrices. I used the function "robust lm" with standard error type "HC3" in version 0.12 of the R package "estimatr" (Blair et al. 2018). I chose the option "HC3" because it is the optimal choice for linear regressions with small sample sizes (MacKinnon and White 1985; Long and Ervin 1998). Using a robust linear regression eliminated the violation of heteroscedasticity and reduced type I error by ensuring standard error estimates (95% confidence intervals) were not underestimated. The slope of each robust linear regression was considered significant for p < 0.05 and $R^2 \ge 0.25$. The restriction on R^2 reduced the likelihood of artificially significant slopes caused by outliers in the dataset. In other words, the explanatory power of the regression would be too low if the regression failed to capture 25% or more of the variance in p-values.

Nestedness

Anti-nested metacommunity structure and high nestedness may not be mutually exclusive, because one value for turnover can have a wide range of nestedness values associated with it (Schmera et al. 2018). In addition to turnover z-scores, I calculated two other measures of species nestedness for each incidence matrix, relativized nestedness (Nrel) and maximum nestedness metric based on overlap and decreasing/differing fill (NODF_{max}) (Almeida-Neto et al. 2008; Podani and Schmera 2012). For two elevational bands (incidence matrix rows) x and z in a matrix with n bands, the number of species the two bands share is *both_{xz}*, the number of species found only in x is *only_x* and the number of species found only in band z is $only_z$. N_{rel} is defined as $\frac{1}{\binom{n}{2}}\sum_{x < z} Nrel_{xz}$ where $Nrel_{xz}$ equals $\frac{both_{xz} + |only_x - only_z|}{both_{xz} + only_x + only_z}$ if $both_{xz}$ is greater than zero and zero otherwise. NODF_{max} is defined as $\frac{1}{\binom{n}{2}}\sum_{x < z} NODF_{xz}$ where $NODF_{xz}$ equals $\frac{both_{xz}}{both_{xz} + \min(only_x, only_z)}$ if $only_x$ does not equal only_z and zero otherwise. The numerator of N_{rel} accounts for the difference in the number of species between elevational bands and how many species two bands have in common. The numerator of NODF_{max}, on the other hand, only reflects how many species are shared between elevational bands. Both metrics assessed the average nestedness of each incidence matrix independent of a latent environmental gradient. N_{rel} and NODF_{max} were both computed in R using the "designdist" function in version 2.4-6 of the "vegan" package (Oksanen et al. 2018). Code for each function was provided in the supplementary material of Schmera et al. (2018).

Abiotic Factors

Four combinations of abiotic predictors were tested for multicollinearity, 1) number of elevational bands and maximum elevation, 2) number of species and number of elevational bands, 3) average annual mean temperature and maximum elevation, and 4) average annual mean temperature and average annual precipitation. The correlation coefficient of each pair was assessed in R with the function "cor". If two predictors had a correlation greater than 0.2 at either local or regional scales, then the two predictors were not used together as covariates in the same multiple linear regression. First, the maximum elevation of a study site may impact the number of 100 meter elevational bands in which at least one species was present. Second, an increase in the number of elevational bands may show a similar increase in the number of species. Third, as elevation increases atmospheric pressure decreases exponentially, resulting in a monotonic decrease in temperature (Jacob 1999). Therefore, the average annual mean temperature for each study site may also decrease across study sites with higher maximum elevation. Forth, average annual mean temperature may be correlated with average annual precipitation.

Assuming the variability in small-mammal habitats increases with an increase in maximum elevation, nestedness metrics will decrease as maximum elevation increases (Hypothesis 1). The distribution of small-mammals can be greatly limited by increased evaporation (Chenoweth 1917), temperature (Pruitt 1959), and even soil texture (Hardy 1945). If temperature and precipitation are limiting factors of species dispersal along elevational gradients, then small-mammal metacommunities will decrease in nestedness (species overlap and species replacements) as temperature and precipitation decrease (Hypothesis 2). All nestedness metrics (dependent variables) were individually modeled

for each taxonomic group with the maximum elevation, average annual mean temperature, or average annual precipitation as predictors (independent variables). As before, I used the function "robust_lm" with standard error type "HC3".

Metacommunity Networks

A metacommunity network was created for each incidence matrix based on a species by species adjacency matrix (Harary 1962) using the function "graph_from_adjacency_matrix" in the R package "igraph" version 1.2.2 with the 'weighted' option as true (Csardi and Nepusz 2006). The adjacency matrix was symmetric with zeros along the diagonal to indicate that species do not have edges connecting to themselves. The off-diagonal entries in the adjacency matrix represent the number of elevational bands species co-occur in. In each metacommunity network an edge connected two nodes every time the two species co-occurred at an elevational band, creating a weighted network of species co-occurrence (Figure 2). The more two species overlap in their elevational range the more edges are drawn between their respective nodes in the metacommunity network. An unweighted network is one in which any redundant edges between two nodes are not drawn. Two species co-occurring at one elevational band is the same as the species co-occurring at multiple elevational bands.

A network is connected when a path of edge traversals exists from a one node to any other node within the network. For metacommunity networks, connected means every species co-occurs with at least one other species at an elevational band. A disconnected network is then one in which there exists a node that cannot be reached by any series of edge transversals, i.e. at least one node is isolated from all others in the network. Connected subsets of nodes in a disconnected network are referred to as

connected components (Allesina et al. 2005; Hopcroft and Tarjan 1973). The nodes in each component are only connected to other nodes within that component, while the components are disconnected from other components in the network.

There are many ways to measure the level of connectivity in a network (Cioabă 2010; Estrada and Benzi 2017; Fiedler 1973). One simple measure of connectivity is vertex connectivity, the minimum number of nodes that must be deleted to separate a connected network into two connected components (Harary and Palmer 1973; Harary 1969). If a network is disconnected, then the vertex connectivity is zero (Figure 3). I defined the species deletion ratio (SDR) as the vertex connectivity divided by the total number of nodes, N, within the network. The maximum number of nodes that can be removed to disconnect a network is N-1, therefore SDR can be at most (N-1)/N. A high SDR implies many species must be removed from the network to disconnect at least one node in the network and the metacommunity network is more connected. SDR is likely to increase as nestedness increases and be associated with nested metacommunity structure.

The vertex connectivity of each network was calculated with the function "vertex_connectivity" also in the "igraph" package in R. The algorithm iterates through all possible node deletions and reports only the minimum number of nodes that must be deleted, but not the identity of these nodes. Deleting a node from the network removes all the edges connected to that node, thus the vertex connectivity is the same for both the weighted and unweighted network. To further understand the impact of species deletions on the metacommunity, the metacommunity structure of all connected components with eight or more species was assessed in MATLAB 2018a by analyzing the incidence matrices with all disconnected species removed. The taxonomic group for each connected

component was not assessed and they were not used in any of the statistical procedures described below.

Species Clusters

A community or species cluster is a set of nodes that share more edges between nodes in the cluster than with nodes outside the cluster. To avoid confusion with the biological definition of "community" I will use the term "cluster" or "species cluster" exclusively. There are many algorithms for identifying clusters in a network, but two common methods are the Louvain method and the Spinglass algorithm (Fortunato and Hric 2016). All disconnected networks were excluded from the process of finding species clusters, because both clustering algorithms required all nodes to be reached from other nodes by edge traversal. Network connectivity was assessed with the function "is.connected" in version 2.4 of the "sna" package in R with the connection option as "strong" (Butts 2016). The term strongly connected is often reserved for networks in which edges have a direction (directed networks) (Khuller, Raghavachari, and Young 1996). In R, however, a strongly connected directed network and a connected undirected network are treated the same.

The Louvain method only requires edge weights as an input parameter. Edge weights were given as the number of edges between two nodes in the weighted metacommunity network. The Louvain method is a hierarchal method based on maximizing the modularity of clusters (Blondel et al. 2008). Modularity is a measure of edges between nodes in a cluster and edges to nodes outside the cluster. The algorithm begins by placing every node in its own cluster then determining the gain in modularity by removing node *i* from its cluster and placing it in the cluster of a directly attached

node. All cluster combinations of neighboring nodes are iterated through and the combinations with the highest modularity are kept. The process of combining clusters continues until no mergers produce a gain in modularity. Species clusters in weighted metacommunity networks were detected with the function "cluster_louvain" in the "igraph" package in R.

The Spinglass algorithm has its roots in statistical physics and is based on the Potts model to identify the spin states of different particles (Potts 1951; Reichardt and Bornholdt 2006). The algorithm uses simulated annealing to minimize the energy function of the network to place nodes in the same spin states or clusters (Kirkpatrick 1984; Traag and Bruggeman 2009; Yang, Algesheimer, and Tessone 2016). To use simulated annealing, the Spinglass algorithm requires a high start and low stop temperature and a small cooling factor. In addition, the parameter "gamma" is required to tell the algorithm how to treat the importance of existing and non-existing edges. When gamma is set to one there is a penalty for non-existing or missing edges between nodes in the same cluster that is equal to the reward for existing edges (Reichardt and Bornholdt 2006). The algorithm further requires a maximum number of spin states or clusters possible. By choosing a reasonably large number of spin states the maximum number of species clusters in the metacommunity can be identified. Extra spin states or clusters will be empty when the algorithm terminates. The Spinglass algorithm is built into the "igraph" package in R with the function "cluster spinglass". The input parameters were a start temperature of 1, stop temperature of 0.01, cooling factor of 0.99, gamma of 1, maximum 25 clusters and used the "simple" update rule.

SDR was used to predict the other three nestedness metrics (turnover z-scores, N_{rel}, and NODF_{max}) to determine if nestedness increases as more species removals were required to disconnect the network (Hypothesis 3). A linear mixed effects model was used with the function "lme" in the R package "nlme" version 3.1-131 by treating study site number as a random effect (Pinheiro et al. 2017). The study site number was an arbitrary label assigned to each study site to allow incidence matrices which share overlapping area to be grouped together. Study site number was treated as categorical in the linear mixed effects model. The number of species clusters was used as a categorical variable in conjunction with SDR if the linear mixed effects model had a significant slope and explained at least 25% of the variance in the nestedness metric (Hypothesis 4). Marginal R^2 values were assessed separately with the function "sem.model.fits" in the R package "piecewiseSEM" (Lefcheck 2016; Nakagawa and Schielzeth 2013). A minimum of ten incidence matrices were required to calculate an intercept adjustment between the number of species clusters. Heteroscedasticity was not controlled for by the linear mixed effects model, but was checked visually by plotting fitted versus residual values. The number of species clusters identified for each network by the two clustering algorithms were compared with a paired Wilcoxon signed rank test in R with the function "wilcox.test".

3. RESULTS

Metacommunity Structures

Fifty-nine literature sources were used to delimit 104 study sites from which 337 incidence matrices were generated. The latent environmental gradient was strongly correlated ($\rho \ge 0.8$) with the elevational gradient in 269 of the 337 incidence matrices (Figure 3). Twenty-three of the 31 disconnected metacommunity networks, however, were not strongly correlated and over half had a correlation below 0.5. Of the 118 local-level incidence matrices 1 was checkerboard, 31 random, 30 anti-nested, 48 quasi-anti-nested, 5 quasi-nested, and 3 nested (Table A1). Of the 219 regional-level matrices, 1 was checkerboard, 19 random, 91 anti-nested, 74 quasi-anti-nested, 31 quasi-nested, and 3 nested (Table A2). The number of species or elevational bands in an incidence matrix did not impact the identification of metacommunity structure (Table 1; Table 2).

Across all local and regional-level incidence matrices 50 (about 15%) were identified as having random metacommunity structure. Twenty-five (half) of the random metacommunity structures had disconnected networks in which one or more species did not overlap with any other species in the assemblage. In other words, the taxonomic group of species resulted in the inclusion of one or more species that shared no elevational band with any other species, thus SDR was zero for these metacommunity networks. Eighteen of the 25 disconnected metacommunity networks with random metacommunity structure had 8 or more species within a connected component. Two metacommunity networks reduced to identical connected components (same species composition) when disconnected species were removed, but all others remained unique. Only 2 connected components remained random, while the other 16 (or 15 excluding the

duplicate connected component) produced a non-random metacommunity structure (Table B1).

Abiotic Factors

The number of elevational bands (rows) was correlated (r>0.2) with the maximum elevation of a study site for both local (r=0.769) and regional (r=0.554) incidence matrices. The number of species (columns) showed a positive correlation with the number of elevational bands (rows) for local-level matrices (r=0.233), but this was not observed at the regional-level (r=0.080). Average annual mean temperature showed a negative correlation with maximum elevation at both scales, local (r=-0.714) and regional (r=-0.276). Average annual mean temperature and average annual precipitation showed a positive correlation at both scales, local (r=0.655). Multiple predictors were not used at either scale to avoid issues with multicollinearity.

None of the four nestedness metrics consistently decreased across taxonomic groups as maximum elevation increased (Tables 3-6). Relativized nestedness and NODF_{max} decreased significantly with a linear increase in maximum elevation in only the local-level superorder taxonomic group. All four nestedness metrics were not significantly correlated with temperature or precipitation across local and regional scales (Tables 7-14). Only relativized nestedness for the local-level multiple superorders group increased significantly and explained more than twenty-five percent of the variance in relativized nestedness values.

Metacommunity Networks

Turnover z-scores decreased significantly as SDR increased at the local-level $(t_{64}=-5.203, p < 0.05)$, but the model fit was poor $(R^2=0.160)$. A significant decrease in turnover z-scores as SDR increased was not detected at the regional-level $(R^2=0.008, t_{167}=1.289, p=0.1)$ (Figure 4). N_{rel} increased at local $(R^2=0.323, t_{64}=7.466, p < 0.05)$ and regional $(R^2=0.342, t_{167}=9.370, p < 0.05)$ scales as SDR increased (Figure 5). NODF_{max} did not show a significant decrease at either local $(R^2=0.028, t_{64}=1.714, p=0.09)$ or regional $(R^2=0.021, t_{167}=1.892, p=0.06)$ scale as SDR increased (Figure 6).

Sixteen local and fifteen regional-level disconnected networks were excluded from species clustering analysis. The number of species clusters determined by the Louvain method was significantly less (W=37, p<0.05) than the number determined by the Spinglass algorithm (Figure 7). The number of species clusters detected by the Louvain method ranged from one to four at both scales. Local-level networks with two and three species clusters had sufficient sample sizes to fit linear mixed effects models to, while regional-level had sufficient sample size for one, two, and three species clusters. The number of clusters in the Spinglass algorithm ranged from one to five, but only networks with two and three species clusters had sufficient sample sizes at both scales. When the number of species clusters was included as a categorical predictor along with SDR, there was no difference in N_{rel} between metacommunity networks with one, two, or three clusters for either clustering algorithm (Table 15; Table 16).

4. DISCUSSION

Metacommunity Structure

The majority of small-mammal metacommunities were quasi-anti-nested and antinested. The elevational gradient was highly correlated ($\rho \ge 0.8$) with the latent environmental gradient (determined via reciprocal averaging) in the majority of metacommunities. Metacommunity structure was not dependent on incidence matrix size, therefore in most cases I can conclude metacommunity structures were likely the result of species-specific responses to changes in the elevational gradient. Elevational gradients often result in different vegetation zones (Kelt 1999; Clausnitzer and Kityo 2001) and are known to cause a peak in species richness and diversity at mid-elevations (Brown 2001; Lomolino 2001; McCain 2004). The high frequency of quasi-anti-nested and anti-nested metacommunity structures was not unexpected as small-mammals are known to track changes in habitat type (Rowe and Terry 2014). A quasi-anti-nested metacommunity structure was also detected for rodents in western Mexico, but the latent environmental gradient was not correlated with the elevational gradient (Lopez-Gonzalez and Lozano 2015).

Metacommunity structure, however, was also dependent on species inclusions and exclusions as the number of species per elevational band directly impacts the possible random matrices used in the null distribution (Gotelli and Graves 1996). More taxonomic groups in one study site may have increased the chance of observing a wider variety of metacommunity structures within that site. Of the 53 local study sites only 14 showed a change in metacommunity structure between different taxonomic groups, while at the regional-level 28 of 51 showed a change. Regional-level study sites typically had a wider

variety of species and allowed for the formation of more taxonomic groups.

The connectedness of the metacommunity network must also be considered when interpreting the results of the metacommunity structure. When one or more species in the metacommunity shares no elevational band with another species then the network is disconnected. Roughly 88% of the disconnected networks with random metacommunity structure changed to a non-random metacommunity structure when disconnected species were removed. The majority of disconnected networks as well showed a low correlation between the elevational gradient and the latent environmental gradient. The reciprocal averaging algorithm was likely unable to place a single disconnected elevational band along the latent gradient without generating too many embedded absences. My findings support previous warnings that species inclusions and exclusions in an assemblage should be based a biological reason (Gotelli and Graves 1996; Gotelli and Ulrich 2012), but this reason likely needs to extend beyond the taxonomy of species. Grouping species by taxonomy alone can generate too many disconnected metacommunity networks and prevent the detection of non-random metacommunity structures.

The definition of nestedness must be clearly understood to use the EMS framework and compare it with other nestedness metrics as well. The original definition asserts nestedness is the loss of species as the environmental gradient is traversed (Darlington 1957; Daubenmire 1975), but there is a wide variety of definitions and metrics for nestedness (Podani and Schmera 2011; Ulrich and Almeida-Neto 2012; Ulrich, Almeida-Neto, and Gotelli 2009; Ulrich and Gotelli 2007). Even though the EMS algorithm reorders elevational bands by reciprocal averaging, it still requires the existence of an environmental gradient. N_{rel} and NODF_{max}, on the other hand, reflect the

average nestedness of an entire metacommunity and will not reflect an environmental gradient, latent or otherwise. Differences in the definition and calculation of nestedness are likely why turnover z-scores showed a wide range of N_{rel} and $NODF_{max}$ values (Figure 8). The broad range of nestedness values for one value of turnover support the conclusions of Gotelli and Ulrich (2012) and Schmera et al. (2018) to use the EMS framework with caution and with other metrics of nestedness.

Abiotic Factors

Maximum elevation was not a significant predictor of any of the four nestedness metrics and could not be associated with metacommunity structures or global patterns of nestedness in this study (Tables 3-6). Increases in maximum elevation may be an insufficient proxy for increases in the diversity of habitats or vegetative zones, resulting in an increase in species turnover and a decrease in nestedness. Using a more sophisticated geographic information system to capture heterogeneity of habitats along each elevational gradients would be a superior approach. The harsh conditions near mountain peaks also make it unlikely for small-mammal communities to occur at the highest elevations. In the central and southern Andes Mountains no species have been detected above 3,500 meters above sea level (masl) (Novillo and Ojeda 2014). Yet, on Mount Kilimanjaro *Dendromus insignis* was detected at the highest sampling point of 4,000 masl and could possibly extend above this elevation (Stanley et al. 2014). Using the maximum sampled elevation instead of maximum elevation in the region would require the highest elevations to be sampled to ensure small-mammal species are absent at these elevations due to an inability to survive in these harsh environments, and not sampling bias.

The impact of habitat change along the elevational gradient on nestedness metrics could be further explored by expanding the geographical scale beyond local and regional. A study of nematodes in European lakes found that increasing the geographical scale from local to supra-regional led to increases in positive turnover (Dümmer, Ristau, and Traunspurger 2016). In desert small-mammal communities, NODF and other metrics of nestedness showed an increase with increasing scale from patch to regional (Rodriguez and Ojeda 2013). Although this study did not allow for direct comparison between scales, only within, it is still an important consideration when interpreting metacommunity structure and nestedness results.

Average annual mean temperature and average annual precipitation did not show any relationship with the four nestedness metrics at either scale (Tables 7-14). Both predictors represent an average of averages, as data from WorldClim were averaged from 1960-1990 then raster cell values were averaged for each study site. This approach may not provide a fine enough resolution to associate either temperature or precipitation with global differences in nestedness. Warm temperatures near the equator cause greater evaporation and more rainfall, but in temperate climates warm summers tend to be dry (Madden and Williams 1978; Rusticucci and Penalba 2000; Trenberth and Shea 2005). Averaging across a year prevents the detection of changes in temperature and precipitation with seasonality.

Exploring new abiotic predictors of nestedness is worthwhile, because global climate change will impact species distributions (Crozier and Dwyer 2006; Moritz et al. 2008; Rowe, Finarelli, and Rickart 2010) and will likely impact the observed nestedness patterns of small-mammals metacommunities. Other abiotic predictors such as the

frequency of seasonal storms or anthropogenic promoters of habitat change may provide greater insights into the maintenance of nested and anti-nested patterns. For example, terrestrial gastropods in Puerto Rico displayed a temporal trend from anti-nested to nested structure following a hurricane (Bloch, Higgins, and Willig 2007). Small-mammals in marshlands disturbed by controlled burns and mowing also showed a loss of nestedness during periods of disturbance (Herczeg and Horvath 2015). Temporal change in nestedness patterns due to disturbance may, however, imply the use of discrete patterns from a limited time frame is inappropriate to assess the vast complexity of metacommunities across scales (Gotelli and Ulrich 2012).

Metacommunity Networks

The nestedness metric I defined, SDR, was a significant predictor of N_{rel} (Figure 5), but not turnover z-scores (Figure 4) or NODF_{max} (Figure 6). A significant increase in SDR with N_{rel} supports the use of SDR to assess nestedness based on species overlap, but could be associated with metacommunity structures. Nestedness was previously explored in relation to modularity for ecological networks and demonstrated a negative correlation between the two that became more pronounced as connectance increased (Fortuna et al. 2010). Connectance was defined as the number of edges divided by the number of possible edges (Fortuna et al. 2010; Rodrigue, Comtois, and Slack 2017). SDR improves on the findings of Fortuna et al. (2010) in two ways. First, modularity is well suited to understanding the clustering of nodes in a network, but does not necessarily imply nestedness. The Louvain method, which relied solely on modularity to create species clusters, did not show a significant decrease in N_{rel} as the number of species clusters increased. Second, a node deletion removes all edges associated with that node, allowing

SDR to be independent of the number of edges between nodes and connectance as defined above. Connectance in a weighted network is unable to capture the differences in edge weights, because calculating the number of possible edges treats all edges as equally possible. SDR is a more appropriate measure of connectedness than connectance in weighted networks.

Small-mammal metacommunity networks with low SDR, however, showed a wide range of N_{rel} values (Figure 5). The wide range of N_{rel} values may argue against SDR as a measure of nestedness, but for its use as an improved measure of connectance. Metacommunities with high N_{rel} and low SDR may have only a few species in the metacommunity connecting nested subsets of species along the elevational gradient. In other words, highly connected subsets of species linked by the dispersal of a few species. Identifying these metacommunities are of great concern as they are likely susceptible to the loss of species interactions or potentially reflect the gain of species interaction through introduced species. Assume two nested communities are connected by only one species. If this species experiences a shift in elevational range not experienced by other species in the metacommunity, then the two nested communities may become disconnected. The loss of species interactions can have severe consequences on ecosystem health and precede species extinctions (Valiente-Banuet et al. 2015). If instead these two nested communities are connected by an introduced species, then previously isolated pathogens may become more common across the gradient (Slenning 2010; Suzan et al. 2015). For example, plague was re-introduced to Madagascar through *Rattus rattus* (Chanteu et al. 1998), a species that has a wide elevation range in d'Anjanaharibe-Sud when compared with endemic species (Goodman and Carleton 1998). Therefore, in
addition to exploring abiotic factors influencing species dispersal, it will be necessary to assess life-history traits of small-mammals and patterns of species introductions to the region. Activity patterns and dietary preference, for example, would distinguish between species that co-occur at an elevation but do not interact and those that are likely in direct competition with one another (Castro-Arellano and Lacher 2009; Pinotti, Naxara, and Pardini 2011). It is also necessary to understand how the individual qualities of species within an assemblage impact their response to habitat changes to further assess the impacts global climate change may have on the nestedness of each system (Moritz et al. 2008).

Conclusion

The majority of small-mammal metacommunities had quasi-anti-nested and antinested metacommunity structure as defined by the EMS framework and showed a strong response to the elevational gradient. Anti-nested metacommunity structures, however, had a wide range of N_{rel} and NODF_{max} values, highlighting the differences in nestedness as defined by species replacements along an environmental gradient and species cooccurrence independent of a gradient. There are many factors that may promote nested metacommunities, but before those mechanisms can be fully assessed it is vital to define what nestedness means and to what extent dynamic processes can be inferred from static patterns. The EMS framework and other nestedness metrics I investigated only depended on species distributions from a short time frame or accumulated records of species presence and absence. Despite these limitations, the nestedness of species clusters should be further explored with metacommunity networks to understand how network connectivity impacts the average nestedness of a metacommunity.

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TABLES

Table 1. Coherence P-values were not Predicted by the Number of Elevational Bands. The slope of each robust linear regression demonstrates that the number of elevational bands in an incidence matrix does not influence p-values for coherence across local or regional scales. Local-level multiple suborders did have a significant p-value but R^2 was not sufficient.

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	-0.664	31	0.51	0.019
	Suborder	-0.978	13	0.35	0.041
	Order	-0.926	17	0.37	0.029
	Superorder	-0.750	8	0.47	0.145
	Mult. Superorders	-2.346	37	0.02	0.076
Regional	Genus	0.336	8	0.75	0.006
	Family	-1.799	57	0.08	0.032
	Suborder	-1.237	25	0.23	0.081
	Order	-1.307	40	0.20	0.013
	Superorder	-1.408	33	0.17	0.028
	Mult. Superorders	-1.518	41	0.14	0.009

Table 2. Turnover P-values were not Predicted by the Number of Species. The slope of each robustlinear regression was not significant (p > 0.05) demonstrating the number of species in an incidence matrixdoes not influence turnover p-values.

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	-1.307	31	0.20	0.043
	Suborder	0.180	13	0.86	0.005
	Order	0.499	17	0.62	0.039
	Superorder	-0.817	8	0.44	0.081
	Mult. Superorders	-1.112	37	0.27	0.019
Regional	Genus	0.628	8	0.55	0.159
	Family	-0.560	57	0.58	0.006
	Suborder	-0.445	25	0.66	0.009
	Order	1.116	40	0.27	0.041
	Superorder	-0.857	33	0.40	0.014
	Mult. Superorders	-0.650	41	0.52	0.004

Table 3. Maximum Elevation was not a significant predictor of Turnover Z-scores. Turnover z-scores for each incidence matrix were not predicted by the maximum elevation in the region across local and regional scales. No slope values were significant (p < 0.05) with sufficient R^2 values ($R^2 > 0.25$).

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	0.834	31	0.41	0.016
	Suborder	2.588	13	0.02	0.202
	Order	0.459	17	0.65	0.014
	Superorder	1.76	8	0.12	0.228
	Mult. Superorders	1.577	37	0.12	0.072
Regional	Genus	0.272	8	0.79	0.008
	Family	0.696	58	0.49	0.012
	Suborder	1.901	25	0.07	0.057
	Order	-0.306	41	0.76	0.002
	Superorder	0.054	33	0.96	0
	Mult. Superorders	1.278	42	0.21	0.053

Table 4. Maximum Elevation did not Predict N_{rel} . The maximum elevation in the region was not a significant predictor of N_{rel} for most incidence matrices. Only local-level incidence matrices grouped by a single superorder had a significant slope for the robust linear regression and sufficient R^2 (value in bold).

Scale	Relatedness	Slope	Т	DF	P-value	R^2
Local	Family	-2.8E-05	-1.081	31	0.29	0.056
	Suborder	-1.4E-05	-0.478	13	0.64	0.017
	Order	-1.4E-05	-0.337	17	0.74	0.012
	Superorder	-6.7E-05	-3.426	8	0.01	0.613
	Mult. Superorders	-3.2E-05	-1.553	37	0.13	0.071
Regional	Genus	-9.0E-05	-2.367	8	0.05	0.496
	Family	-1.4E-05	-0.768	58	0.45	0.012
	Suborder	-3.3E-06	-0.105	25	0.92	0.001
	Order	-4.6E-05	-2.444	41	0.02	0.122
	Superorder	-3.7E-05	-1.469	33	0.15	0.057
	Mult. Superorders	-4.6E-05	-2.456	42	0.02	0.112

Table 5. Maximum Elevation did not Predict NODF_{max}. The maximum elevation in the region was not a significant predictor of NODF_{max} for most incidence matrices. Only local-level incidence matrices grouped by a single superorder showed significant slope of the linear regression and sufficient R^2 (value in bold).

Scale	Relatedness	Slope	Т	DF	P-value	R^2
Local	Family	-3.7E-05	-1.260	31	0.22	0.079
	Suborder	-6.9E-06	-0.231	13	0.82	0.003
	Order	-4.7E-06	-0.099	17	0.92	0.001
	Superorder	-6.6E-05	-4.697	8	< 0.05	0.518
	Mult. Superorders	-9.8E-06	-0.319	37	0.75	0.004
Regional	Genus	-6.0E-05	-1.341	8	0.22	0.261
	Family	3.8E-05	1.909	58	0.06	0.073
	Suborder	5.9E-05	1.606	25	0.12	0.124
	Order	1.6E-05	0.374	41	0.71	0.010
	Superorder	1.8E-05	0.961	33	0.34	0.020
	Mult. Superorders	3.3E-05	1.151	42	0.26	0.067

Table 6. Maximum Elevation did not Predict SDR. Maximum elevation in the region was not a

significant predictor of SDR at both local and regional scales.

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	-0.202	31	0.84	0.002
	Suborder	0.993	13	0.34	0.110
	Order	0.702	17	0.49	0.061
	Superorder	0.216	8	0.83	0.006
	Mult. Superorders	-0.405	37	0.69	0.005
Regional	Genus	-1.958	8	0.09	0.455
	Family	-0.522	58	0.60	0.006
	Suborder	0.916	25	0.37	0.040
	Order	-1.791	41	0.08	0.082
	Superorder	-0.661	33	0.51	0.019
	Mult. Superorders	-1.851	42	0.07	0.086

 Table 7. Temperature did not Predict Turnover Z-scores. Average annual mean temperature was not a significant predictor of turnover z-scores at either local or regional scales. The slope of the robust linear regression fit to each relatedness grouping was not significantly different from zero.

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	0.124	31	0.90	~ 0
	Suborder	-0.076	13	0.94	0.001
	Order	-0.405	17	0.69	0.011
	Superorder	-1.065	8	0.32	0.152
	Mult. Superorders	-1.228	37	0.23	0.041
Regional	Genus	1.160	8	0.28	0.125
	Family	-1.147	58	0.26	0.025
	Suborder	-1.654	25	0.11	0.175
	Order	-1.768	41	0.08	0.060
	Superorder	-1.059	33	0.30	0.030
	Mult. Superorders	-1.985	42	0.05	0.094

Table 8. Temperature did not Predict Nrel. Average annual mean temperature was not a significantpredictor of Nrel at either local or regional scales. The slope of the robust linear regression fit to eachrelatedness grouping was not significantly different from zero.

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	-0.307	31	0.76	0.005
	Suborder	-0.036	13	0.97	0.000
	Order	-0.381	17	0.71	0.010
	Superorder	2.180	8	0.06	0.445
	Mult. Superorders	0.091	37	0.93	~ 0
Regional	Genus	-1.533	8	0.16	0.363
	Family	-1.318	58	0.19	0.031
	Suborder	0.268	25	0.79	0.005
	Order	0.545	41	0.59	0.011
	Superorder	1.436	33	0.16	0.103
	Mult. Superorders	1.651	42	0.11	0.083

Table 9. Temperature did not Predict NODF_{max}. Average annual mean temperature was not a significant predictor of $NODF_{max}$ at either local or regional scales. The slope of the robust linear regression fit to each relatedness grouping was not significantly different from zero or the amount of variation explained by the regression was not sufficient. Only the regional suborder grouping was close to explaining at least 25% of the variance in the data.

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	-0.034	31	0.97	~ 0
	Suborder	-0.151	13	0.88	0.001
	Order	-0.875	17	0.39	0.062
	Superorder	0.986	8	0.35	0.109
	Mult. Superorders	-1.265	37	0.21	0.045
Regional	Genus	-0.611	8	0.56	0.083
	Family	-2.354	58	0.02	0.088
	Suborder	-2.588	25	0.02	0.242
	Order	-0.815	41	0.42	0.022
	Superorder	-0.984	33	0.33	0.053
	Mult. Superorders	-2.221	42	0.03	0.131

 Table 10. Temperature did not Predict SDR. Average annual mean temperature was not a significant

 predictor of SDR at either local or regional scales. The slope of the robust linear regression fit to each

 relatedness grouping was not significantly different from zero.

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	-0.799	31	0.43	0.033
	Suborder	-0.860	13	0.41	0.140
	Order	-0.459	17	0.65	0.010
	Superorder	-0.816	8	0.44	0.079
	Mult. Superorders	0.590	37	0.56	0.010
Regional	Genus	-1.159	8	0.28	0.122
	Family	-1.188	58	0.24	0.022
	Suborder	-0.247	25	0.81	0.004
	Order	1.146	41	0.26	0.027
	Superorder	1.307	33	0.20	0.040
	Mult. Superorders	1.540	42	0.13	0.058

 Table 11. Precipitation did not Predict Turnover Z-scores. Average annual precipitation was not a

 significant predictor of turnover z-scores at either local or regional scales. The slope of the robust linear

 regression fit to each relatedness grouping was not significantly different from zero.

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	0.550	31	0.59	0.012
	Suborder	0.806	13	0.43	0.070
	Order	0.703	17	0.49	0.024
	Superorder	-0.546	8	0.60	0.071
	Mult. Superorders	-0.795	37	0.43	0.013
Regional	Genus	0.299	8	0.77	0.006
	Family	-0.661	58	0.51	0.012
	Suborder	-1.296	25	0.21	0.155
	Order	-1.038	41	0.31	0.021
	Superorder	-0.768	33	0.45	0.012
	Mult. Superorders	-0.733	42	0.47	0.020

Table 12. Precipitation did not Predict N_{rel} . Average annual precipitation was only a significant predictor of N_{rel} for the local-level relatedness grouping of multiple superorders (t-score in bold). The trend more

frequently observed was no relationship between average annual precipitation and N_{rel}

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	1.228	31	0.23	0.061
	Suborder	-0.171	13	0.87	0.005
	Order	0.438	17	0.67	0.010
	Superorder	1.344	8	0.22	0.307
	Mult. Superorders	4.255	37	< 0.05	0.290
Regional	Genus	-0.846	8	0.42	0.099
	Family	-1.318	58	0.19	0.025
	Suborder	-0.350	25	0.73	0.006
	Order	0.249	41	0.80	0.002
	Superorder	0.821	33	0.42	0.040
	Mult. Superorders	1.471	42	0.15	0.068

Table 13. Precipitation did not Predict $NODF_{max}$. Average annual precipitation was not a significant predictor of $NODF_{max}$ at either local or regional scales. The slope of the robust linear regression fit to each relatedness grouping was not significantly different from zero.

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	1.006	31	0.32	0.054
	Suborder	0.606	13	0.56	0.025
	Order	1.013	17	0.33	0.051
	Superorder	0.503	8	0.63	0.054
	Mult. Superorders	1.250	37	0.22	0.048
Regional	Genus	0.140	8	0.89	0.001
	Family	-0.393	58	0.70	0.003
	Suborder	-1.367	25	0.18	0.091
	Order	-0.201	41	0.84	0.001
	Superorder	-0.303	33	0.76	0.008
	Mult. Superorders	-1.235	42	0.22	0.043

Table 14. Precipitation did not Predict SDR. Average annual precipitation was not a significant predictor of SDR at either local or regional scales. The slope of the robust linear regression fit to each relatedness grouping was not significantly different from zero or the amount of variance explained by the regression was not sufficient. Only the grouping of multiple superorders at the local and regional scales had a significant slope, but the regressions failed to explain a sufficient amount of variance in the data.

Scale	Relatedness	Т	DF	P-value	R^2
Local	Family	0.542	31	0.59	0.010
	Suborder	-0.313	13	0.76	0.013
	Order	0.726	17	0.48	0.023
	Superorder	-0.955	8	0.37	0.105
	Mult. Superorders	2.202	37	0.03	0.110
Regional	Genus	-0.579	8	0.58	0.035
	Family	-0.153	58	0.88	~ 0
	Suborder	0.651	25	0.52	0.041
	Order	1.737	41	0.09	0.086
	Superorder	1.662	33	0.11	0.121
	Mult. Superorders	2.601	42	0.01	0.154

Table 15. The Number of LV Clusters Showed No Difference in N_{rel} . At the local-level, SDR was a significant predictor of N_{rel} , but intercept adjustments were not significant. There was no difference in the nestedness of metacommunity networks with one (Intercept 1), two (Intercept 2), or three (Intercept 3) species clusters as determined by the Louvain method. Intercept 2 was treated as the reference category in at both scales.

Fixed Effect	Estimate	Τ	DF	P-value
Slope	0.341	6.387	49	< 0.05
Intercept 2	0.613	23.094	49	< 0.05
Intercept 3	-0.023	-0.796	49	0.43
Slope	0.290	7.709	149	< 0.05
Intercept 1	0.050	1.766	149	0.08
Intercept 2	0.621	33.514	149	< 0.05
Intercept 3	-0.006	-0.306	149	0.76
	Fixed Effect Slope Intercept 2 Intercept 3 Slope Intercept 1 Intercept 2 Intercept 3	Fixed Effect Estimate Slope 0.341 Intercept 2 0.613 Intercept 3 -0.023 Slope 0.290 Intercept 1 0.050 Intercept 3 -0.023	Fixed Effect Estimate T Slope 0.341 6.387 Intercept 2 0.613 23.094 Intercept 3 -0.023 -0.796 Slope 0.290 7.709 Intercept 1 0.050 1.766 Intercept 2 0.621 33.514 Intercept 3 -0.006 -0.306	Fixed Effect Estimate T DF Slope 0.341 6.387 49 Intercept 2 0.613 23.094 49 Intercept 3 -0.023 -0.796 49 Slope 0.290 7.709 149 Intercept 1 0.050 1.766 149 Intercept 2 0.621 33.514 149 Intercept 3 -0.006 -0.306 149

Table 16. The Number of SG Clusters Showed No Difference in N_{rel} . At the local-level, SDR was a significant predictor of N_{rel} , but intercept adjustment was not significant. There was no difference in the nestedness of metacommunity networks with two (Intercept 2) or three (Intercept 3) species clusters as determined by the Spinglass algorithm.

Scale	Fixed Effect	Estimate	Т	DF	P-value
Local	Slope	0.322	5.790	49	< 0.05
	Intercept 2	0.631	22.748	49	< 0.05
]	Intercept 3	0.007	0.277	49	0.78
Regional	Slope	0.333	8.633	143	< 0.05
	Intercept 2	0.600	31.154	143	< 0.05
	Intercept 3	0.026	1.770	143	0.0788

FIGURES



Figure 1. Metacommunity Network Example. The metacommunity network consists of species (s1 to s10) linked through co-occurrence in at the same elevational band on a given gradient. Edge width is weighted by the number of times two species coincide at an elevational band. Node size is scaled by the total number of edges connecting to the node. Species s1 is connected to five other species at only one site, whereas species s5 and s6 connect with every other species at multiple sites.





Figure 2. Vertex Connectivity. Vertex connectivity represents the number of nodes (species) that must be removed from the network to disconnect it. In the figure a) the vertex connectivity is one because only *Dipodomys merriami* needs to be deleted to disconnect the network into two connected components. In figure b) the network is already disconnected so the vertex connectivity is zero. Even though removing *Cryptotis goodwini* would divide the network into four connected components, the algorithm only looks to break the network into at least two connected components.



Figure 3. Elevation is Highly Correlated with the Latent Environmental Gradient. The majority of incidence matrices (80%) showed a strong correlation ($\rho \ge 0.8$) between elevation in meters and the component score of each elevational band as determined by reciprocal averaging. Yet, only 8 of the 31 disconnected networks (26%) showed a high correlation. Every elevational band represents 100 meters of elevation along the gradient, e.g. 40 elevational bands reflect 4,000 meters of elevation.



Figure 4. Turnover Z-Scores Are Not Significantly Related to SDR. Turnover z-scores decreased significantly as the species deletion ratio (SDR) increased at a) the local-level ($R^2=0.160$, $t_{64}=-5.203$, p<0.05) in the linear mixed effects model with study site treated as a random effect. A significant decline in nestedness as SDR increased was not observed at b) the regional-level ($R^2=0.008$, $t_{167}=1.289$, p=0.1).



Figure 5. N_{rel} **Increases as SDR Increases.** Species deletion ratio (SDR) was a significant predictor of N_{rel} at both scales, a) local ($R^2=0.323$, $t_{64}=7.466$, p<0.05) and b) regional ($R^2=0.342$, $t_{167}=9.370$, p<0.05) in the linear mixed effects model with study site treated as a random effect.



Figure 6. NODF_{max} and SDR Show No Relationship. The species deletion ratio was not a significant predictor of NODF_{max} at either a) local ($R^2=0.028$, $t_{64}=1.714$, p=0.09) or b) regional ($R^2=0.021$, $t_{167}=1.892$, p=0.06) scales in the linear mixed effects model with study site treated as a random effect.



Figure 7. Louvain Found Less Clusters than Spinglass. An example of the output for Louvain (left) and Spinglass (right) clustering algorithms on weighted metacommunity networks. Edge weights are not displayed to improve the ease of viewing. The metacommunity networks in a) and b) represent the same local-level incidence matrix with family relatedness grouping and Clementsian metacommunity structure. The vertex connectivity is three and SDR is about 19%. The regional-level incidence matrix in c) and d) show how close the two algorithms often came to the same solution. The species assemblage was grouped by superorder and had Clementsian metacommunity structure, with a vertex connectivity of nine and SDR of 27%.



Figure 8. Anti-nested Metacommunities Have a Wide Range of Nestedness Values. Turnover z-scores at both local (left) and regional (right) scales had a wide range of values for N_{rel} and NODF_{max}. Turnover z-scores as well did not show a strong negative correlation with either nestedness metric (r in left-hand corner). The results demonstrate that anti-nested metacommunity structures (significant positive turnover z-scores) can be highly nested under different definitions of nestedness. The EMS framework requires an environmental gradient, while N_{rel} and NODF_{max} do not.

APPENDIX SECTION

Appendix A

Table A1. List of All Local-level Incidence Matrices. The study site location, relatedness assemblage (multiple meaning multiple superorders), metacommunity structure (MCS), number of species in the assemblage (NS), the connectedness of the metacommunity network (NET; connected or disconnected), and the reference where source data can be found are listed below. Full reference in Appendix C. Study sites in bold showed a change in identified metacommunity structure due to taxonomic relatedness.

Study Site	Assemblage	MCS	NS	NET	Reference
Cumbres Calchaquíes, Argentina	Cricetidae	Quasi-anti-nested	15	Con	Ferro and Barquez 2009 Ferro and Barquez 2014
	Multiple	Quasi-anti-nested	16	Con	
Diamante, Central Andes, Mendoza Province, Argentina	Cricetidae	Quasi-anti-nested	10	Con	Novillo and Ojeda 2014
Las Lenas, Central Andes, Mendoza Province, Argentina	Cricetidae	Random	9	Con	Novillo and Ojeda 2014
Nevados del Aconquija, Argentina	Cricetidae	Quasi-anti-nested	12	Con	Ferro and Barquez 2009 Ferro and Barquez 2014
	Multiple	Quasi-anti-nested	13	Con	
Sierras de Tilcara, Provincia de Jujuy, Argentina	Cricetidae	Random	16	Dis	Ferro and Barquez 2014
-	Rodentia	Random	17	Dis	
	Multiple	Quasi-anti-nested	19	Con	
Sierras de Zenta, Provincia de Salta, Argentina	Cricetidae	Quasi-anti-nested	17	Con	Ferro and Barquez 2014
	Rodentia	Quasi-anti-nested	18	Con	
	Multiple	Quasi-anti-nested	19	Con	
Tunuyan, Central Andes, Mendoza Province, Argentina	Cricetidae	Random	9	Con	Novillo and Ojeda 2014
Uspallata, Central Andes, Mendoza Province, Argentina	Cricetidae	Quasi-anti-nested	8	Con	Novillo and Ojeda 2014

Table A1. Continued <i>Study Site</i>	Assemblage	MCS	NS	NET	Reference
Mt Lewis, Queensland, Australia	Muridae	Quasi-anti-nested	10	Con	Bateman et al. 2010
	Multiple	Quasi-anti-nested	15	Con	
Itatiaia National Park, Brazil	Cricetidae	Quasi-anti-nested	17	Con	Geise et al. 2014
	Rodentia	Quasi-anti-nested	25	Con	
	Euarchontoglires	Quasi-anti-nested	31	Con	
	Didelphidae	Nested	10	Con	
	Multiple	Quasi-anti-nested	53	Con	
Mineracao Rio Tinto Reunidas, Brazil	Cricetidae	Anti-nested	10	Con	Caceres et al. 2011
	Rodentia	Anti-nested	11	Con	
	Multiple	Anti-nested	17	Con	
MMX Corumba Mineracao, Brazil	Rodentia	Anti-nested	8	Dis	Caceres et al. 2011
	Multiple	Anti-nested	12	Con	
La Picada, Osorno, Chile	Multiple	Quasi-anti-nested	9	Con	Patterson, Meserve, and Lang 1989
Gucheng, China	Rodentia	Quasi-anti-nested	9	Con	Li, Song, and Zeng 2003
	Euarchontoglires	Quasi-anti-nested	12	Con	
Jingteshang, China	Euarchontoglires	Anti-nested	9	Con	Li, Song, and Zeng 2003
Qomolangma National Nature Reserve, China	Muridae	Quasi-anti-nested	9	Con	Hu et al. 2017
	Myomorpha	Anti-nested	12	Con	
	Euarchontoglires	Anti-nested	15	Con	
	Multiple	Anti-nested	18	Con	
Xishui, China	Myomorpha	Anti-nested	8	Con	Li, Song, and Zeng 2003
	Euarchontoglires	Quasi-anti-nested	10	Con	
Tilaran Mtns, Costa Rica	Cricetidae	Random	11	Con	McCain 2004
	Myomorpha	Random	12	Con	
	Rodentia	Quasi-anti-nested	14	Con	
	Multiple	Quasi-anti-nested	16	Con	
Chilalo–Galama, Arsi, Ethiopia	Muridae	Anti-nested	12	Con	Kasso, Bekele, and Hemson 2010
	Multiple	Anti-nested	15	Con	

Table A1. Continued <i>Study Site</i>	Assemblage	MCS	NS	NET	Reference
d'Ambre, Madagascar	Multiple	Nested	8	Con	Goodman et al. 1996
d'Andohahela, Madagascar	Tenrecidae	Random	15	Dis	Goodman, Jenkins, and Pidgeon 1999
	Multiple	Random	16	Dis	
d'Andohahela, Madagascar	Nesomyidae	Random	8	Dis	Goodman, Carleton, and Pidgeon 1999
	Myomorpha	Random	9	Con	
	Multiple	Random	9	Dis	
d'Andringitra, Madagascar	Multiple	Random	8	Dis	Goodman, Raxworthy, and Jenkins 1996
d'Andringitra, Madagascar	Myomorpha	Quasi-anti-nested	8	Con	Goodman and Carleton 1996
d'Anjanaharibe- Sud, Madagascar	Tenrecidae	Random	8	Dis	Goodman and Jenkins 1998 (R-transect)
d'Anjanaharibe- Sud, Madagascar	Microgale	Random	8	Con	Goodman and Jenkins 1998 (V-transect)
	Multiple	Random	9	Con	
d'Anjanaharibe- Sud, Madagascar	Afrotheria	Random	8	Dis	Goodman and Jenkins 1998 (S-transect)
	Multiple	Random	9	Dis	
d'Anjanaharibe- Sud, Madagascar	Nesomyidae	Quasi-anti-nested	8	Con	Goodman and Carleton 1998
	Myomorpha	Random	9	Con	
	Euarchontoglires	Random	10	Con	
	Multiple	Random	17	Con	
Marojejy, Madagascar	Microgale	Quasi-nested	12	Con	Goodman and Jenkins 2000
	Tenrecidae	Quasi-anti-nested	15	Con	
Marojejy, Madagascar	Myomorpha	Quasi-anti-nested	8	Con	Carleton and Goodman 2000
	Multiple	Quasi-anti-nested	12	Con	
Kedah, Malaysia	Rodentia	Quasi-anti-nested	9	Con	Langham 1983
	Euarchontoglires	Quasi-anti-nested	10	Con	
	Multiple	Quasi-anti-nested	11	Con	
Mt Kinabalu, Sabah, Malaysia	Rodentia	Random	9	Con	Nor 2001
	Euarchontoglires	Random	11	Con	
	Multiple	Anti-nested	12	Con	
Sierra Mazateca, Oaxaca, Mexico	Cricetidae	Anti-nested	16	Con	Sánchez-Cordero 2001
	Rodentia	Anti-nested	17	Con	

Study Site	Assemblage	MCS	NS	NET	Reference
Sierra Mixteca, Oaxaca, Mexico	Cricetidae	Anti-nested	21	Con	Sánchez-Cordero 2001
	Rodentia	Anti-nested	23	Con	
Camiguin Island, Philippines	Multiple	Nested	8	Con	Heaney et al. 2006
Mt Isarog, Calabanga, Philippines	Multiple	Quasi-nested	8	Con	Rickart, Heaney and Utzurrum 1991
Mt Kitanglad, Mindanao, Philippines	Muridae	Quasi-anti-nested	8	Con	Heaney 2001
	Multiple	Quasi-anti-nested	10	Con	
Zambales Mtns, Luzon, Phillipines	Muridae	Anti-nested	9	Con	Balete et al. 2009
	Multiple	Anti-nested	11	Con	
Volcanoes National Park, Rwanda	Multiple	Quasi-anti-nested	11	Con	Tuyisingize et al. 2013
Drakensberg Mtns, South Africa	Myomorpha	Quasi-anti-nested	9	Con	Armstrong and van Hensbergen 1996
	Rodentia	Quasi-anti-nested	10	Con	
	Multiple	Quasi-anti-nested	13	Con	
Giant's Castle Game Reserve, South Africa	Multiple	Quasi-nested	9	Con	Rowe-Rowe and Meester 1982
Guanshan, Taiwan	Multiple	Random	8	Con	Yu 1994
Yushan, Taiwan	Multiple	Quasi-anti-nested	8	Con	Yu 1994
Mt Maru, Tanzania	Rodentia	Anti-nested	8	Con	Stanley and Kihaule 2016
	Multiple	Anti-nested	10	Con	
Mt Kilimanjaro, Tanzania	Myomorpha	Quasi-anti-nested	9	Con	Stanley et al. 2014
	Rodentia	Quasi-anti-nested	10	Con	
	Multiple	Quasi-anti-nested	16	Con	
Ruaha National Park, Tanzania	Muridae	Random	11	Dis	Stanley, Rogers, and Kihaule 2015
	Myomorpha	Quasi-nested	15	Dis	
	Rodentia	Random	17	Dis	
	Multiple	Random	20	Dis	

Table A1. Continued

Table A1. Continued	Assamblaga	MCS	NS	NFT	Patavanca
Udzungwa Mtns, Tanzania	Muridae	Quasi-anti-nested	10	Con	Stanley et al. 2005
	Myomorpha	Quasi-anti-nested	11	Con	
	Multiple	Anti-nested	18	Con	
Udzungwa Mtns, Tanzania	Muridae	Quasi-anti-nested	14	Con	Stanley and Hutterer 2007
	Soricidae	Quasi-anti-nested	9	Con	
	Multiple	Quasi-anti-nested	23	Con	
Mt Elgon, Uganda	Muridae	Anti-nested	9	Con	Clausnitzer and Kityo 2001
	Myomorpha	Anti-nested	12	Con	
Rwenzori, Uganda	Soricidae	Checkerboard	8	Dis	Kerbis Peterhans et al. 1998
	Laurasiatheria	Random	10	Con	
	Muridae	Quasi-anti-nested	10	Con	
	Myomorpha	Anti-nested	13	Con	
	Rodentia	Anti-nested	14	Con	
	Multiple	Anti-nested	25	Con	
Deep Canyon Transect, Colorado Desert, California, USA	Rodentia	Quasi-anti-nested	11	Con	Kelt 1999
Ruby, Nevada, USA	Myomorpha	Quasi-nested	8	Con	Rowe, Finarelli and Rickart 2010
	Rodentia	Random	16	Con	
	Multiple	Random	23	Con	
Ruby, Nevada, USA	Cricetidae	Random	9	Con	Borell and Ellis 1934 Rowe, Finarelli, and Rickart 2010
	Myomorpha	Random	10	Con	
	Rodentia	Anti-nested	21	Con	
	Euarchontoglires	Anti-nested	22	Con	
	Multiple	Anti-nested	25	Con	

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Table A2. List of All Regional-level Incidence Matrices. The study site location, relatedness assemblage (multiple meaning multiple superorders), metacommunity structure (MCS), number of species in the assemblage (NS), the connectedness of the metacommunity network (NET; connected or disconnected), and the reference where source data can be found are listed below. Full reference in Appendix C. Study sites in bold showed a change in identified metacommunity structure due to taxonomic relatedness.

Study Site	Assemblage	MCS	NS	NET	Reference
Central Andes, Mendoza Province, Argentina	Cricetidae	Anti-nested	14	Con	Novillo and Ojeda 2014
Northwest Argentina	Akodon	Quasi-anti-nested	8	Con	Ferro and Barquez 2009 Ferro and Barquez 2014
	Cricetidae	Quasi-anti-nested	29	Con	
	Rodentia	Quasi-anti-nested	31	Con	
	Multiple	Quasi-anti-nested	34	Con	
Urucum Mtns, Brazil	Cricetidae	Anti-nested	10	Con	Caceres et al. 2011
	Rodentia	Anti-nested	12	Con	
	Multiple	Anti-nested	19	Con	
Mt Cameroon, Cameroon & Nigeria + Bioko Island, Equatorial Guinea	Muridae	Quasi-anti-nested	13	Con	Cronin et al. 2014
	Rodentia	Quasi-anti-nested	14	Con	
	Multiple	Quasi-anti-nested	21	Con	
Costa Rica	Reithrodontomys	Quasi-anti-nested	8	Con	McCain 2006
	Cricetidae	Anti-nested	29	Con	
	Rodentia	Anti-nested	35	Con	
Bale Mtns, Ethiopia	Muridae	Anti-nested	10	Con	Clausnitzer and Kityo 2001 Yalden 1988
	Myomorpha	Anti-nested	14	Con	
	Multiple	Anti-nested	19	Con	
Chebera Churchura National Park, Ethiopia	Muridae	Quasi-nested	12	Con	Datiko and Bekele 2014
	Multiple	Quasi-nested	14	Con	
Menagesh State Forest, Ethiopia	Muridae	Quasi-anti-nested	8	Con	Bekele 1996
	Myomorpha	Anti-nested	10	Con	
	Rodentia	Quasi-anti-nested	11	Con	
	Multiple	Quasi-anti-nested	12	Con	

Table A2. ContinuedStudy Site	Assemblage	MCS	NS	NET	Reference
Mt Qilian, China	Myomorpha	Anti-nested	13	Con	Li, Song, and Zeng 2003
	Rodentia	Quasi-anti-nested	15	Con	2005
	Euarchontoglires	Anti-nested	18	Con	
Nothern Central America, Guatemala & Honduras	Cryptotis	Random	8	Dis	Woodman et al. 2012
	Soricidae	Random	12	Disc	
Sulawesi, Indonesia	Sciuridae	Anti-nested	9	Con	Musser et al. 2010 Musser 2014
	Bunomys	Anti-nested	8	Con	
	Rodentia	Anti-nested	17	Con	
d'Ambre, Madagascar	Tenrecidae	Quasi-anti-nested	8	Con	Goodman et al. 1996
	Multiple	Quasi-nested	13	Con	
d'Andohahela, Madagascar	Microgale	Anti-nested	10	Con	Goodman, Carleton, and Pidgeon 1999 Goodman, Jenkins, and Pidgeon 1999
	Tenrecidae	Random	15	Disc	-
	Nesomyidae	Random	8	Disc	
	Myomorpha	Random	9	Con	
	Multiple	Random	26	Con	
d'Andringitra, Madagascar	Microgale	Quasi-nested	11	Con	Goodman and Carleton 1996 Goodman and Rasolonandrasana 2001 Goodman, Raxworthy, and Jenkins 1996
	Tenrecidae	Quasi-anti-nested	16	Con	
	Nesomyidae	Quasi-anti-nested	9	Con	
	Myomorpha	Anti-nested	11	Con	
	Strepsirrhini	Random	12	Dis	
	Euarchontoglires	Quasi-anti-nested	23	Con	
	Multiple	Quasi-anti-nested	39	Con	

Study Site	Assemblage	MCS	NS	NET	Reference
d'Anjanaharibe-Sud, Madagascar	Microgale	Quasi-nested	9	Con	Goodman and Carleton 1998 Goodman and Jenkins 1998
	Tenrecidae	Quasi-nested	11	Con	
	Nesomyidae	Quasi-anti-nested	8	Con	
	Myomorpha	Random	9	Con	
	Euarchontoglires	Random	10	Con	
	Multiple	Quasi-nested	21	Con	
Marojejy, Madagascar	Microgale	Quasi-nested	12	Con	Goodman and Jenkins 2000 Carleton and Goodman 2000
	Tenrecidae	Quasi-anti-nested	15	Con	
	Myomorpha	Quasi-anti-nested	8	Con	
	Euarchontoglires	Quasi-anti-nested	23	Con	
Mt Kinabalu, Sabah, Malaysia	Sciuridae	Quasi-nested	21	Con	Nor, 2001
·	Muridae	Quasi-anti-nested	21	Con	
	Rodentia	Quasi-anti-nested	43	Con	
	Euarchontoglires	Quasi-anti-nested	47	Con	
	Multiple	Quasi-anti-nested	53	Con	
El Cielo Biosphere Reserve, Tamaulipas, Mexico	Cricetidae	Anti-nested	16	Con	Sabate and Paniagua 2002
	Rodentia	Anti-nested	26	Con	
	Euarchontoglires	Anti-nested	28	Con	
	Caniformia	Anti-nested	9	Con	
	Laurasiatheria	Anti-nested	12	Con	
	Multiple	Anti-nested	40	Con	
La Sepultura Biosphere Reserve, Chiapas, Mexico	Cricetidae	Quasi-anti-nested	10	Con	Sabate and Paniagua 2002
	Rodentia	Quasi-anti-nested	19	Con	
	Euarchontoglires	Quasi-anti-nested	20	Con	
	Caniformia	Quasi-nested	9	Con	
	Euarchontoglires	Quasi-nested	29	Con	
North-West Oaxaca, Mexico	Peromyscus	Anti-nested	9	Con	Sanchez-Cordero 2001
	Cricetidae	Anti-nested	24	Con	
	Rodentia	Anti-nested	26	Con	

Table A2. ContinuedStudy Site	Assemblage	MCS	NS	NET	Reference
Sierra de Atoyac de Alvarez, Guerrero, Mexico	Cricetidae	Quasi-anti-nested	12	Con	Sabate and Paniagua 2002
1.200000	Rodentia	Quasi-nested	15	Con	
	Euarchontoglires	Quasi-nested	16	Con	
	Multiple	Quasi-nested	22	Con	
Sierra Gorda, Queretaro, Mexico	Cricetidae	Quasi-anti-nested	19	Con	Sabate and Paniagua 2002
-	Rodentia	Quasi-nested	30	Con	
	Euarchontoglires	Quasi-nested	31	Con	
	Laurasiatheria	Quasi-nested	9	Con	
	Multiple	Quasi-nested	42	Con	
Sierra de Juarez, Oaxaca, Mexico	Cricetidae	Quasi-anti-nested	18	Con	Sabate and Paniagua 2002
	Rodentia	Quasi-anti-nested	22	Con	
	Multiple	Quasi-anti-nested	32	Con	
New Guinea	Dasyuridae	Anti-nested	13	Con	Rickart 2001
	Peramelidae	Anti-nested	9	Con	
	Phalangeridae	Anti-nested	9	Con	
	Pseudocheiridae	Quasi-anti-nested	9	Con	
	Phalangeriformes	Quasi-anti-nested	25	Con	
	Diprotodontia	Quasi-anti-nested	27	Con	
	Marsupialia	Anti-nested	49	Con	
	Rattus	Quasi-anti-nested	14	Con	
	Muridae	Quasi-nested	70	Con	
	Multiple	Nested	121	Con	
New Guinea Highlands, Egna Province, Papua New Guinea	Muridae	Quasi-nested	11	Con	Helgen 2007
	Phalangeriformes	Quasi-anti-nested	9	Con	
	Diprotodontia	Quasi-anti-nested	12	Con	
	Marsupialia	Quasi-anti-nested	19	Con	
	Multiple	Quasi-anti-nested	31	Con	
Manu Biosphere Reserve, Manu, Peru	Didelphidae	Quasi-nested	17	Con	Solari et al. 2006 Pacheco et al. 1993
	Muridae	Anti-nested	25	Con	
	Hystricomorpha	Random	13	Dis	
	Rodentia	Quasi-anti-nested	43	Con	
	Euarchontoglires	Quasi-anti-nested	44	Con	
	Multiple	Quasi-nested	78	Con	

Study Site	Assemblage	MCS	NS NET		Reference	
Mt Isarog, Luzon, Philippines	Multiple	Nested	8	Con	Rickart, Heaney, and Utzurrum 1991	
Mt Kitanglad, Sumilao, Bukidnon, Philippines	Muridae	Anti-nested	10	Con	Musser and Heaney 1992	
	Myomorpha	Anti-nested	13	Con		
	Euarchontoglires	Anti-nested	14	Con		
	Multiple	Anti-nested	17	Con		
Mt Kitanglad, Mindanao, Philippines	Multiple Anti-nested		18	Con	Heaney 2001 Musser and Heaney 1992	
Yushan, Taiwan	Multiple	Anti-nested	9	Con	Yu 1994	
Yushan National Park, Taiwan	Multiple	Anti-nested	9	Con	Yu 1994	
Rwenzori, Uganda	Soricidae	Quasi-anti-nested	8	Con	Kerbis Peterhans et al. 1998	
	Laurasiatheria	Quasi-anti-nested	13	Con		
	Muridae	Quasi-anti-nested	18	Con		
	Myomorpha	Quasi-anti-nested	21	Con		
	Rodentia	Quasi-anti-nested	25	Con		
	Multiple	Anti-nested	40	Con		
Aquarius Mtns, Arizona, USA	Cricetidae	Anti-nested	13	Con	Rickart 2001	
	Myomorpha	Anti-nested	14	Con		
	Sciuridae	Anti-nested	9	Con		
	Rodentia	Anti-nested	23	Con		
	Euarchontoglires	Anti-nested	27	Con		
	Multiple	Anti-nested	30	Con		
Deep Canyon, California USA	Heteromyidae	Random	8	Con	Shepherd and Kelt 1999	
	Castorimorpha	Quasi-nested	9	Con		
	Cricetidae	Quasi-anti-nested	10	Con		
	Rodentia	Anti-nested	24	Con		
	Euarchontoglires	Anti-nested	27	Con		
	Multiple	Anti-nested	29	Con		
Ruby Mtns, Nevada, USA	Cricetidae	Quasi-nested	10	Con	Rickart 2001	
	Myomorpha	Quasi-nested	11	Con		
	Rodentia	Quasi-anti-nested	20	Con		
	Euarchontoglires	Quasi-anti-nested	25	Con		
	Multiple	Quasi-anti-nested	27	Con		

Table A2. Continued

Study Site	Assemblage	MCS	NS	NET	Reference
Snake Mtns, Nevada, USA	Cricetidae	Quasi-anti-nested	10	Con	Rickart 2001
	Rodentia	Quasi-anti-nested	23	Con	
	Euarchontoglires	Quasi-nested	27	Con	
	Multiple	Quasi-anti-nested	29	Con	
Deep Creek Range, Nevada & Utah, USA	Cricetidae	Anti-nested	11	Con	Rickart 2001
	Rodentia	Anti-nested	24	Con	
	Euarchontoglires	Anti-nested	29	Con	
Abajo Mtns, Utah, USA	Rodentia	Anti-nested	15	Con	Rickart 2001
	Euarchontoglires	Anti-nested	17	Con	
	Multiple	Anti-nested	21	Con	
Fishlake, Utah, USA	Cricetidae	Anti-nested	12	Con	Rickart 2001
	Myomorpha	Anti-nested	13	Con	
	Sciuridae	Quasi-anti-nested	10	Con	
	Rodentia	Anti-nested	26	Con	
	Euarchontoglires	Anti-nested	33	Con	
	Multiple	Anti-nested	36	Con	
Henry, Utah, USA	Cricetidae	Quasi-anti-nested	9	Con	Rickart 2001
	Rodentia	Quasi-anti-nested	16	Con	
	Euarchontoglires	Quasi-anti-nested	18	Con	
La Sal, Utah, USA	Cricetidae	Quasi-anti-nested	8	Con	Rickart 2001
	Myomorpha	Anti-nested	9	Con	
	Rodentia	Anti-nested	18	Con	
	Euarchontoglires	Quasi-anti-nested	22	Con	
	Multiple	Quasi-anti-nested	26	Con	
	Cricetidae	Anti-nested	10	Con	
Markagunt, Utah, USA	Lagomorpha	Anti-nested	19	Con	Rickart 2001
	Rodentia	Random	8	Dis	
	Euarchontoglires	Anti-nested	27	Con	
	Multiple	Anti-nested	29	Con	
	Multiple	Anti-nested	30	Con	

Table A2. Continued

Study Site	Assemblage	MCS	NS	NET	Reference
Oquirrh Mtns, Utah, USA	Cricetidae	Random	10	Con	Rickart 2001
	Myomorpha	Quasi-anti-nested	11	Con	
	Rodentia	Anti-nested	19	Con	
	Euarchontoglires	Quasi-anti-nested	21	Con	
Pavant, Utah, USA	Cricetidae	Random	9	Con	Rickart 2001
	Myomorpha	Quasi-anti-nested	10	Con	
	Rodentia	Quasi-anti-nested	19	Con	
	Euarchontoglires	Quasi-anti-nested	24	Con	
	Multiple	Quasi-anti-nested	26	Con	
	Multiple	Anti-nested	24	Con	
Raft River Mtns, Utah, USA	Cricetidae	Random	11	Dis	Rickart 2001
	Myomorpha	Checkerboard	12	Dis	
	Rodentia	Random	24	Dis	
	Euarchontoglires	Quasi-nested	28	Dis	
	Multiple	Random	30	Dis	
Stansbury Mtns, Utah, USA	Cricetidae	Quasi-anti-nested	11	Con	Rickart 2001
	Rodentia	Nested	20	Dis	
	Euarchontoglires	Random	23	Dis	
	Multiple	Random	26	Dis	
Tushar, Utah, USA	Cricetidae	Quasi-anti-nested	9	Con	Rickart 2001
	Myomorpha	Anti-nested	10	Con	
	Rodentia	Anti-nested	19	Con	
	Euarchontoglires	Anti-nested	26	Con	
	Multiple	Anti-nested	29	Con	
Uinta, Utah, USA	Cricetidae	Anti-nested	15	Con	Rickart 2001
	Myomorpha	Anti-nested	16	Con	
	Sciuridae	Anti-nested	10	Con	
	Rodentia	Anti-nested	32	Con	
	Lagomorpha	Anti-nested	9	Con	
	Euarchontoglires	Anti-nested	41	Con	
	Multiple	Anti-nested	46	Con	

Table A2. Continued

Study Site	Assemblage	MCS	NS	NET	Reference
Wasatch Plateau, Utah, USA	Cricetidae	Anti-nested	12	Con	Rickart 2001
	Myomorpha	Anti-nested	13	Con	
	Rodentia	Anti-nested	23	Con	
	Lagomorpha	Anti-nested	8	Con	
	Euarchontoglires	Anti-nested	31	Con	
	Multiple	Anti-nested	34	Con	
Wasatch Range, Utah, USA	Cricetidae	Quasi-anti-nested	12	Con	Rickart 2001
	Myomorpha	Quasi-anti-nested	13	Con	
	Rodentia	Quasi-anti-nested	22	Con	
	Lagomorpha	Anti-nested	8	Con	
	Euarchontoglires	Anti-nested	30	Con	
	Multiple	Anti-nested	34	Con	
Great Smoky Mountains National Park, USA	Cricetidae	Quasi-anti-nested	14	Con	Linzey 2016
	Myomorpha	Quasi-anti-nested	19	Con	
	Rodentia	Quasi-nested	26	Con	
	Euarchontoglires	Quasi-nested	28	Con	
	Soricidae	Anti-nested	8	Con	
	Soricomorpha	Anti-nested	11	Con	
	Laurasiatheria	Anti-nested	16	Con	
	Multiple	Quasi-nested	45	Con	

Appendix B

Table B1. Connected Components of Disconnected Networks with Random MCS. All the study sites listed were disconnected networks identified as having random metacommunity structure, but one of their connected components had at least eight species to re-evaluate the metacommunity structure. CCMCS – Connected Component Metacommunity Structure; ONS – Original Number of Species; CCNS – Connected Component Number of Species. Full reference in Appendix C. The metacommunity network that reduced to identical connected components is in bold.

Study Site	Scale	CCMCS	ONS	CCNS	Reference
Sierras de Tilcara, Provincia de Jujuy, Argentina	Local	Clementsian	16	15	Ferro and Barquez 2014
		Clementsian	17	16	
Guatemala & Honduras	Regional	Quasi-anti-nested	12	11	Woodman et al. 2012
d'Andohahela, Madagascar	Local	Clementsian	15	13	Goodman, Jenkins, and Pidgeon 1999
		Clementsian	16	13	
d'Andohahela, Madagascar	Local	Random	9	8	Goodman, Carleton, and Pidgeon 1999
d'Andohahela, Madagascar	Regional	Clementsian	15	13	Goodman, Jenkins, and Pidgeon 1999 Goodman, Carleton, and Pidgeon 1999
d'Andringitra, Madagascar	Regional	Quasi-nested	12	11	Goodman and Rasolonandrasana 2001 Goodman, Raxworthy, and Jenkins 1996 Goodman and Carleton 1996
d'Anjanaharibe-Sud, Madagascar	Local	Random	9	8	Goodman and Jenkins 1998 (S-transect)
Manu Biosphere Reserve, Manu, Peru	Regional	Nested	13	11	Solari et al. 2006 Patterson, Meserve and Lang 1989
Ruaha National Park, Tanzania	Local	Quasi-anti-nested	11	10	Stanley, Rogers, and Kihaule 2015
		Quasi-anti-nested	17	16	
		Quasi-nested	20	19	
Raft River Mtns, Utah, USA	Regional	Nested	11	10	Rickart 2001
		Quasi-anti-nested	24	22	
		Quasi-anti-nested	30	28	
Stansbury Mtns, Utah, USA	Regional	Quasi-nested	23	22	Rickart 2001
		Quasi-anti-nested	26	25	

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