

Staphylinid diversity and community structure across a neotropical elevation gradient

by

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ABSTRACT

STAPHYLINID DIVERSITY AND COMMUNITY STRUCTURE ACROSS A NEOTROPICAL ELEVATION GRADIENT

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Environmental stress from abiotic conditions imposes physiological limits on communities. Stressful conditions can act as environmental filters on the individuals present in an assemblage or taxa available to colonize a given habitat. This can reduce a community's diversity and make its composition more phylogenetically clustered. I tested this prediction using rove beetles (Staphylinidae, Coleoptera) collected across an elevation gradient in northwestern Costa Rica. Using DNA barcodes and phylogenetic estimates of community structure, I found high species turnover across elevation, and that staphylinid diversity (measured both through barcodes and phylogenetically) increased linearly with elevation. This diversity was negatively related to surface area and temperature, and positively with precipitation. I suggest that historical biogeography, rather than contemporary environmental stress alone, has produced these diversity patterns.

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CHAPTER 1: Prologue

How is biodiversity distributed, and what affects its structure? What are the mechanisms that alter these patterns? Despite a long history of investigation, uncertainties remain about these patterns and the environmental mechanisms that can alter them. In areas of the world where we have limited understanding of biodiversity (Gotelli, 2004), this uncertainty is accentuated. With climate change already altering some of these most understudied areas and taxa, it is important to describe and catalogue these patterns and to test potential mechanisms behind them (Colwell et al., 2008).

In my thesis I study one of the most diverse and abundant terrestrial animals, the rove beetles (Coleoptera, Staphylinidae), across an elevation gradient in Costa Rica. I describe their abundance, diversity, and phylogenetic community structure across this gradient, and test their relationship to some of the most influential drivers of biodiversity: area, temperature, and precipitation.

1.1 Elevation Gradients

Predicting the exact response of a particular species to changing abiotic conditions is not trivial (Keller et al., 2013). So much so that Palmer (1994) reviewed over 120 hypotheses that have been presented to explain patterns in species diversity with environmental conditions. For any single investigator to evaluate all these hypotheses is not feasible, so I have elected to start with large-scale environmental factors as a reasonable first foray into a system. The reasoning behind this decision is simple: on broad community scales (such as biome) abiotic factors are the largest predictors of community composition (Hutchinson, 1957; Grubb, 1977). This is because abiotic factors not only influence community structure but also influence biotic interactions (See Niche Theory: Grinnell, 1917; Hutchinson, 1957). Specifically that the range of a species is a result of environmental variation, interspecific variation, and the interaction between these. In my thesis I follow principles from Niche Theory.

To test how environmental factors affect communities, I use gradients. Ecological gradients represent continuous changes in multiple environmental factors, thus allowing for direct comparisons of taxonomic groups under different ecological conditions. For example, elevation gradients show changes in temperature and precipitation across almost all mountain ranges

(McCain & Grytness, 2010). The degree of these changes varies based on latitude, whether the mountains are part of a mountain range or isolated, or proximity to an ocean. Tropical areas (roughly (but not exclusively) between the tropic of Capricorn (23.3° S) and the Tropic of Cancer (23.5° N)) have smaller fluctuations in temperature than temperate latitudes. Janzen (1967) made the influential observation that the ranges of species in the tropics are determined more by the size of the temperature gradient across that mountain than on the size of the elevation gradient (Ghalambor et al., 2006). This temperature dependence results in greater specialization to smaller niches and a reduction in successful dispersal out of that environment (Janzen, 1967). Janzen's logical extrapolation in 1967 was that the different climates between the valleys and mountain passes of tropical mountain ranges creates a dramatic barrier to species whose physiology has evolved in a the (relatively) uniform climatic zone (Janzen, 1967). Consequently tropical mountains therefore have greater turnover in habitat and inhabitant communities compared to temperate mountains of comparable size (Janzen, 1967; Ghalambor et al., 2006; Sheldon, Yang & Tewksbury, 2011). Additionally, mountain ranges have effects on elevational gradients that are not observed on isolated mountains. Isolated mountains have smaller and lower borders of different forests (particularly tropical montane cloud forests) than mountains within mountain ranges, described as the Massenerhebung effect (Grubb, 1971). This is due to mountain ranges having cloud cover higher up in the mountain than isolated mountains, increasing water in the soil and slowing organic matter mineralization, thus lowering the borders between lower and upper forest types (Grubb, 1971).

1.2 Diversity

While there are many ways of characterizing diversity, perhaps the most frequently used is taxonomic richness (the number of different taxa in an area) where taxon is frequently a species. Diversity is subsequently partitioned into regional diversity (or gamma (γ) diversity) where alpha (α) diversity is the diversity within a site, and beta (β) diversity is between different sites (Chazdon, 2011).

To calculate richness and diversity you have to first define the community to be investigated. Defining a community implies that the organisms living within these community boundaries interact with each other. Therefore, defining too large a community does not make biological sense and may imply a relationship that does not exist, and too small a community will miss interactions. For example, to examine the effect of temperature and precipitation, the community must be broad enough to encompass the whole resident assemblage in that

temperature range, but also narrow enough that it does not encompass other climatic communities (Swenson et al., 2006).

For studies examining community change across elevation, a community is often defined as an elevation band or category. In tropical environments these bands are narrow with high turnover between them and the assemblages within are characterized by specialization to the reduced variability in environmental conditions (Janzen, 1967; Grubb, 1971). It is likely that while most species inhabiting specific elevation bands can move about within these climatic bands and interact with these organisms, it is less likely that they can disperse and interact with organisms outside of these bands. For the purpose of my study, I have defined a community as the assemblage of species found at a given elevational sampling site.

1.3 The Taxonomic Impediment and DNA Barcodes

Species richness and diversity are useful metrics to describe ecosystems, however it is a less useful metric in taxa where species are not yet formally described or named (Smith, Fisher & Hebert, 2005). This problem is one axis of the taxonomic impediment, where some groups are largely undescribed, are poorly understood, have cryptic biology, and/or have a paucity of taxonomists studying them (Gotelli, 2004; *Canadian Taxonomy: Exploring Biodiversity, Creating Opportunity*, 2010; Smith, 2012). These problems are amplified in the tropics due to the diversity present here, where many taxa are under sampled or undescribed, and collections can be dominated by singletons and doubletons (species collected only once or twice) (Gotelli, 2004).

One type of taxonomic impediment, taxonomic cypsis, can be avoided by using molecular methods of species identification, specifically DNA barcode divergence (Barcode Index Numbers: BINs) as a proxy for calculations of taxon richness (Ratnasingham & Hebert, 2007; Janzen et al., 2009). Barcode Index Numbers (BINs) are a DNA-barcode based delineation based on patterns of intra- and inter- specific nucleotide variation in the Cytochrome c oxidase subunit I (COI) gene, outlined by Ratnasingham & Hebert (2013). The BIN system uses the Refined Single Linkage (RESL) to align sequences, cluster sequences based on similarities, and delineate operational taxonomic unit (OTU) boundaries. RESL additionally examines the previously established barcode library through a random walk to account for and incorporate topological information and cluster records with high connectivity.

The BIN system was specifically designed to rapidly compute these delineations and make the erection of species-proxy hypotheses transparent and rapid. BINs allow a researcher to delineate a species-proxy even in the absence of a formal description - a factor that is especially important when working with neotropical arthropods where many are cryptic and undescribed (Hamilton et al., 2010).

1.4 Phylogenetic Community Structure

Ecological communities do not just differ by the species they contain, but also by how those species are related; their phylogenetic diversity (PD) and their phylogenetic community structure (PCS). Described by Faith (1992) and Crozier (1992), PD is a way of quantifying diversity using the minimum branch length between an assemblage of taxa on a phylogenetic tree. Mean pairwise distance (MPD – the shortest paths that connect a subset of species) and mean nearest taxon distance (MNTD – average distance that connects a subset of species) are other commonly used measures of phylogenetic and functional diversity. Some literature has suggested that PD is a more informative way to characterize diversity in a community as it represents a quantification of the diversity and history of traits in an area as opposed to taxonomic names (Crozier, 1992; Faith, 1992). Crozier (1992) and Crozier, Agapow & Smith (2008) also suggests that in the face of economic limitations in conservation, preserving phylogenetic diversity or genetic diversity is the most economic choice to make.

If phylogeny and function are coupled, using phylogenetic metrics not only allows one to quantify diversity but can also help to infer ecological information about these communities. For example, if the species present in a community are more closely related phylogenetically than you would expect by chance, it may indicate that traits are shared (Webb et al., 2002). One explanation commonly offered to explain this pattern is environmental stress (Webb et al., 2002; Zwerschke et al., 2013). If functionality and phylogeny are coupled, then species present in stressful environments may possess a trait, or traits, that enable their persistence, thus resulting in phylogenetic clustering. However, one should not immediately presume that a single chain of cause and effect exists when other factors, such as interspecific competition, can produce communities less related than expected by chance due to competitive exclusion (Swenson, 2013; Cadotte & Tucker, 2017). It is unlikely that ecological differences are influenced by only one trait in response to one environmental factor, but it also is unlikely that it is a large number of traits (Cadotte, Davies & Peres-Neto, 2017). Regardless of the ecological mechanisms that have

driven these patterns, they are reflecting phylogenetic differences and thus may be reflecting differences that have been evolved (Cadotte, Davies & Peres-Neto, 2017).

Phylogenetic community structure and environmental filtering theories have been used since publications such as Clements (1916) and Ricklefs (1987), but since the seminal Webb et al. (2002) manuscript described it, the use of PCS concepts (measured through citations of Webb et al. (2002)) has increased exponentially (Fig S1). In response to the increase in studies using PCS, the recent literature has explored some caveats of the original predictions in detail. For example, if individuals within the same niche experience local exclusion (such as interspecific competition), this can result in eliminating or extirpating species from a given area (Cadotte & Tucker, 2017). The result is minimum niche overlap of coexisting species, appearing as phylogenetic dispersion. The same pattern could also be a result of distantly related species having converged based on similar niche use. Thus, it is possible that factors such as competition or environmental filtering are affecting the same community at once, resulting in patterns of phylogenetic evenness or overdispersion due to convergent evolution (Stayton, 2015; Cadotte & Tucker, 2017). Convergent evolution is the independent evolution of similar traits in response to some environmental factor or habitat resulting in separate lineages (Ghiselin, 2018). Finally, environmentally filtered communities may not show phylogenetic clustering since a species may be maintained in an environment simply through immigration from an external source (Cadotte & Tucker, 2017).

Spatial scale plays an important role in determining and interpreting phylogenetic community structure (Webb et al., 2002; Swenson et al., 2006; Vanoverbeke, Urban & De Meester, 2016). Vamosi et al. (2009) discussed how a community defined at different spatial scales will be influenced by different mechanisms that affect diversity and community structure. For example, on larger spatial scales biogeographical influences (historical) rather than ecological influences (circumstance) explain the diversification of certain species in an area (Webb et al., 2002; Vamosi et al., 2009). The species present in this given area would then be more related on average in comparison to other species on a global phylogeny (Webb et al., 2002).

Phylogenetic community structure is useful, but it is important to not ignore factors of growth, dispersal, and trait correlations with phylogenetic community structure because these in combination with traditional methods could provide informative inferences (Kraft et al., 2015; Cadotte & Tucker, 2017). A meta-analysis using 258 cross taxa phylogenetic community

structure studies by Kraft et al. (2015) found that only 40% of the studies that found evidence of phylogenetic clustering looked at the actual species traits or ability to tolerate these harsh environments. While ignoring species traits is not ideal, the problem is that what we can learn from PCS studies is most pronounced amongst the taxa for which we know the least – arthropods (Smith, 2015). In many of these taxa, estimates of growth, dispersal, and other functional traits are not well known and difficult to quantify. The value of measuring and describing PCS in these taxa, despite unknowns about their ecological traits, is more important than not studying it at all (Swenson, 2013; Smith, 2015).

1.5 Conservation and Climate Change

Phylogenetic diversity has been called the raw material for adaptation to changing environmental conditions (Crozier, 1992; Faith, 1994), a phenomenon critical to understanding a world affected by anthropogenic climate change. Tropical montane ecosystems are currently experiencing proportionally larger increases in temperature and reduced precipitation than temperate systems (Mora et al., 2013). Lawton et al. (1998) argued that conservation measures are useless if we do not first create a baseline from which to assess changes. Studying diversity and phylogenetic community structure across elevation gradients in the tropics are thus not only important to simply describe these patterns before they are eliminated or altered, but also to infer conservation approaches once those patterns are understood (Faith, 1992, 1994; Anderson & Ashe, 2000).

Understanding species diversity and species ranges across temperature gradients is useful because climate change threatens to change this diversity and the ranges in which this diversity is present. Shifts in climate will not affect all species ranges equally, causing the decoupling of species interactions (Schweiger et al., 2008). This is especially relevant on elevation gradients where individuals at the lowest and highest elevations do not have lower or higher habitats to which they can migrate and seek refuge (Colwell et al., 2008; Sheldon, Yang & Tewksbury, 2011). New, altered, or lost species interactions due to range shifts and consequent temporal mismatching could limit a species' or community's ability to persist (Schweiger et al., 2008).

1.6 The Rove Beetles (Staphylinidae)

The rove beetles (Coleoptera, Staphylinidae) are one of the largest families of insects, (and possibly eukaryotic animals) worldwide (Betz, Irmeler & Klimaszewski, 2018).. They are present in an enormous range of terrestrial habitats and ecosystems (Brunke et al., 2011; Betz, Irmeler & Klimaszewski, 2018). There are currently over 63,000 staphylinid species described, and the estimated number of undescribed species is much greater, so that even a conservative estimate would predict that there are more staphylinid species than all vertebrate species (Betz, Irmeler & Klimaszewski, 2018). With such great diversity and so many undescribed species, much about their natural history and ecology remains to be discovered. Despite this, some generalizations can be made. Irmeler & Gurlich (2007) demonstrated that staphylinid diversity is positively influenced by microhabitat diversity. Staphylinids also tend to be more abundant in moist habitats (Newton & Thayer, 1992; Qodri, Raffiudin & Noerdjito, 2016). Pohl, Langor, & Spence (2007) and Bohac (1999) showed that staphylinid diversity is influenced by a forest's age and disturbance levels. Staphylinids may also be a useful indicator family for the erection of conservation priorities because staphylinids are present in most terrestrial ecosystems (Bohac, 1999; Anderson & Ashe, 2000).

Due to the few described species relative to the diversity of the family, few studies focus on the staphylinids compared with other hyperdiverse beetle families. This is primarily because staphylinids are diverse and un-described (Gutiérrez-Chacon et al., 2009; Betz, Irmeler & Klimaszewski, 2018). Our understanding of staphylinid phylogenetic systematics has seen recent changes (Brunke et al., 2011). For example, two groups of beetles formerly placed in their own families have recently been grouped as subfamilies of Staphylinidae (Pselaphinae, and Scydmaeninae). Such large taxonomic changes make many older identification resources obsolete. Recent progress has been made, including keys to staphylinid subfamilies of Eastern Canada and the United States by Brunke et al. (2011).

CHAPTER 2: Staphylinid diversity and community structure across a neotropical elevation gradient

2.1 Introduction

The biodiversity of a community and how it is structured between different communities is determined by many individual environmental factors and complex interactions. Isolating which of these factors influence diversity, and in what way, is not trivial, because there are more potential mechanisms than there are ways to test them (See: Palmer, 1994). One proposed mechanism driving community formation and structure is that of increasing environmental stress (i.e. the amount of negative force that the abiotic environment exerts on the physiological performance of a group in a community (Zwerschke et al., 2013)). For ectotherms, temperature and precipitation are important in maintaining homeostasis (Marshall, 2006). Consequently, extreme moisture and temperature can impose physiological stress (Chatzaki et al., 2005). Additionally, resource availability can be dependent on temperature and precipitation, and therefore limited in stressful environments (Huston, 1979; Lawton, Macgarvin & Heads, 1987; Chatzaki et al., 2005). This can therefore change a community's structure because inhabitants of stressful environments must be tolerant of these extreme conditions (Scrosati et al., 2011; Zwerschke et al., 2013). One potential explanation for this trend is the possession of a particular trait, or set of traits, that allows taxa to exist despite these stressors, and therefore the dominance of a few species which possessed this trait (or traits) (Huston, 1979). Environmental filtering is a local environmental restriction, such as environmental stress, which leads to the persistence of a few specialized species (Kraft et al., 2007). If habitat use is a conserved trait, or if this specialization (trait or traits) is phylogenetically coupled, then the taxa present may be phylogenetically clustered (more closely related than by chance).

Reduced diversity and evidence of phylogenetic clustering have been reported in physically stressful environments (see: (Vamosi et al., 2009)– particularly those associated with elevation (Machac et al., 2011; Hoiss et al., 2012; Smith, Hallwachs & Janzen, 2014). For example, Heino et al. (2015) found that maximum temperature was negatively related to variation in beetle phylogenetic diversity and increased phylogenetic clustering. Alternatively, Barraclough, Hogan, & Vogler (1999) found no evidence that beetle community structure changed across habitat types or climatic condition, and Smith (2015) who examined the prevalence of high-elevation phylogenetic clustering across many ant studies, found no clear trend for this family.

Patterns in diversity may arise simply due to geographic boundaries (i.e. area), regardless of environmental boundaries or gradients (Rahbek, 1995; Colwell & Lees, 2000). Larger areas generally having higher species richness (Arrhenius, 1921; Rosenzweig, 1994; Lomolino, 2000). As area increases, the relative importance of immigration and extinction decreases while the importance of evolutionary processes like *in situ* speciation increases. Larger areas tend to have a greater number of available niches and thus habitat availability (He & Legendre, 1996). As such, these larger areas can even be the source populations for these smaller areas. Species-area trends can be studied on mountains due to their (simplified) conical shape. Across elevation, particularly in the tropics (Janzen, 1967), these area changes can be looked at through island biogeography theory because of changes in elevation, which have consequent changes in area and climatic shifts, thus making elevation bands similar to insular environments (MacArthur & Wilson, 1967). As such, larger areas (lower elevations) may tend to be the source populations for smaller (higher elevation) areas (MacArthur & Wilson, 1967). Some research has focused on the effects of area changes across elevation on insect populations. Sanders (2002) found available area was a significant determinant of ant species richness, while Lawton et al. (1987) found that species diversity patterns of insect herbivores with habitat was only significant when area was included as a covariate.

One way to understand the impact that environmental factors can have on community composition is to test the change in species composition across ecological gradients (McCain & Grytness, 2010; Sanders & Rahbek, 2012). An ecological gradient is one where there are continuous changes in multiple environmental factors (such as those associated with latitude or elevation). Elevational gradients are useful to test the role of environmental factors in determining community composition, but on a smaller spatial gradient than latitude (Rahbek, 1995; McCain & Grytness, 2010; Sanders & Rahbek, 2012). As elevation increases many abiotic factors change, particularly temperature and precipitation (McCain & Grytness, 2010). Changes in temperature and precipitation control the generation of biomass across elevations and thus influence community diversity and structure (McCoy, 1990). These patterns are more exaggerated on isolated, tropical mountains due to fewer events of climatic uniformity from the tips to the base of the mountains (Janzen, 1967), and lower cloud immersion thus lowering the border between different habitats (Grubb, 1971).

2.1.1 Model System

The Área de Conservación Guanacaste (ACG) is a 165,000 hectare UNESCO world heritage preserve located in northwestern Costa Rica containing 3 stratovolcanoes (www.gdfcf.org). Due to their height and location, abiotic conditions across these volcanoes change drastically. As elevation increases, precipitation increases and temperature decreases. For example, the lapse rate maximum temperature across this gradient is approximately 1 °C for every 100 m (Smith in prep). Due to this, there are three distinct forest types across the gradient (Smith, Hallwachs & Janzen, 2014). Low elevations are hot and dry (dry forests), making them physically stressful for organisms needing moisture. High elevations (tropical montane cloud forests) are cold and wet making them physically stressful for ectotherms. Mid-elevations (rain forests) are a mixture of these two environments being hot and moist, and would thus be the least environmentally stressful and likely would have the highest species richness (McCain & Grytness, 2010).

Insects are a good model to investigate trends of community structure because they occupy a wide range of habitats and are strongly influenced by climatic niches (Stork, 1993). Rove beetles (Coleoptera: Staphylinidae) are one of the most diverse families of insects (Bohac, 1999). Staphylinids have been shown to be sensitive to changes in habitats (Bohac, 1999; Pohl, Langor & Spence, 2007). In the tropics, staphylinids are extremely abundant and diverse in leaf litter and present in a wide variety of niches (Anderson & Ashe, 2000). In tropical forests it has been suggested they be used as a model taxon to determine conservation priorities (See: Anderson & Ashe, 2000).

Several taxa have been evaluated along the elevational gradient in the ACG (ants, Collembola, isopods, wasps - (Smith, Hallwachs & Janzen, 2014; Smith et al., 2015), however staphylinids within the ACG have not been studied before. Thus, to evaluate staphylinid diversity and community structure we must attempt to first characterize and quantify the diversity of staphylinids in the ACG, and then test predictions regarding the effect of abiotic conditions on these communities. My goal in this thesis was to ask two questions: How many and which staphylinid species are present within the ACG? How do the abiotic factors that co-vary with elevation, (area, precipitation and temperature) affect the richness, and phylogenetic structure of these neotropical staphylinid communities?

2.1.2 Hypotheses and Predictions

- 1) Staphylinid diversity should be related to the amount of available area due to larger areas having more habitat heterogeneity and thus more available niches. Thus, if staphylinid diversity is related to area, then diversity will decrease as elevation increases across a conical mountain.
- 2) Staphylinid richness is influenced by environmental stress imposed by temperature and precipitation due to the thermal tolerance of staphylinids. If mid-elevations have the least physically stressful temperatures and levels of precipitation, then staphylinid diversity and abundance will be highest at mid-elevations.
- 3) Phylogenetic structure of staphylinids is determined by an environmental filter which is selecting species to only those that possess a trait that enables presence in physically stressing environments. If abiotic stressors impose an environmental filter on staphylinids, then species at high and low elevations will be more closely related than predicted by chance.

2.2 Methods

2.2.1 Location and Sampling

Beetles were derived from collections made over a decade of sampling in the ACG between 2008 and 2017 along elevational transects established from sea level to the summit of the volcano Cacao (Smith, Hallwachs & Janzen, 2014). The transect crosses 3 distinct forest types (tropical dry forest, tropical rain forest, and montane cloud forest) across eight collection sites (Fig. 1). Throughout this time, sampling was performed by M. Alex Smith and members of the Smith lab. The standardized sampling regime has been described by Smith, Hallwachs & Janzen (2014). I participated in the sampling conducted in April of 2017. Briefly, sampling was standardized to characterize the arthropod fauna using pitfall traps, Davis-sifting of the leaf litter, mini-Winkler sifting of the leaf-litter, bait, active searching and Malaise traps. Malaise traps are maintained year round at each site and are emptied weekly. Specimens from all collection methods were preserved in 95% ethanol upon collection and later preserved at -20 °C.

2.2.2 Abiotic Factors

To calculate the surface area of each elevational band, I used topographic data of Costa Rica from The Earth Observing System Data and Information System (EOSDIS; <<https://earthdata.nasa.gov/>>) and downloaded the Digital Elevation Model (DEM) into ArcGIS (<<http://www.esri.com>>). Pre-made shape files of all of the individual terrestrial protected areas in the ACG were downloaded (with thanks to Waldy Medina, ACG, available from <https://www.acguanacaste.ac.cr/biodesarrollo/sistemas-de-informacion-geografica>). These projections were then defined and matched to the EOSDIS land data using the spatial reference CR LAMBERT NORTE. I categorized the topographic data into 100 m elevation bands, starting at -50 m to 50 m to 1850 – 1950 m above sea level. I used categories starting at 50 m in order to surround the elevation sites that are typically on the 100 m (Fig 1; i.e. the 600 m elevation site will be represented by the surface area from 550 to 650 m). Surface area of each elevation was then extracted for each elevation band. Staphylinids were grouped into these elevation bands based upon every elevation site where they were present.

Temperature was recorded at each site since 2013 (each 15 minutes) using Hobo RG3M and Pendant data loggers. From these, I used daily average, maximum and minimum temperatures (Smith et al. in prep). I extracted mean annual precipitation data from each of the 8 elevation sites using Worldclim - Global Climate data from 1960-1990 (<http://www.worldclim.org>; (Hijmans et al., 2005)).

2.2.3 Staphylinidae Sampling

All collections from Volcan Cacao containing beetles were subsequently sorted to Staphylinidae. Documents from Mckenna et al. (2015) and Herman (2001) were used as identification resources as staphylinid taxonomy has undergone recent changes where previously separate families have subsequently been moved to sub-families within Staphylinidae (i.e. Scydmaeinae (Mckenna et al. (2015) and Herman (2001))).

From all staphylinid collections made between 2008 and 2017 in the ACG, I calculated abundance for each of the 8 elevation sites. Of the staphylinids sampled, I identified most to subfamily using a key to staphylinid genera in Mexico Navarrete-Heredia et al. (2002) and a key to subfamilies of Eastern Canada and United States by Brunke et al. (2011).

2.2.4 Tissue Sampling, DNA Sequencing, and Amplification

All specimens were pointed for preservation and tissue sampling. Three high-resolution focus-stacked photographs were taken of each specimen under a Leica Z16 AP0A microscope using Leica Application Software V4.3 at three orientations (dorsal, lateral, and anterior head).

Total genomic DNA was extracted from 2-6 legs depending on beetle size. Mitochondrial DNA from the 5' region of the cytochrome *c* oxidase I (COI) gene (the animal DNA barcode locus) was amplified and sequenced using standard methods (Ivanova, Dewaard & Hebert, 2006; Smith et al., 2009) at the Biodiversity Institute of Ontario. DNA sequences and trace files were then uploaded to the Barcode of Life Data System (BOLD; www.barcodinglife.org; Ratnasingham & Hebert, 2007). Where sequencing failed or produced amplicons of low-quality, samples were re-amplified using primers that amplified a smaller portion of the same locus (i.e. 400 bp rather than 650 bp). Successful mini-amplicons were sequenced at the University of Guelph Genomics Facility.

Sequences with large numbers of ambiguities were reviewed and edited in Sequencher 5.4.1 (Sequencher, 2015). I aligned all sequences using MUSCLE (Edgar, 2004) in MEGA6 (Tamura et al., 2013), and BioEdit (Hall, 1999). Aligned and edited sequences were uploaded to the Barcode of Life Data System (Ratnasingham & Hebert, 2007).

2.2.5 Alpha Diversity

To quantify staphylinid diversity, I used DNA barcodes. One measure of diversity (taxon richness) was quantified using Barcode Index Numbers (BINs). BINs are a specific type of molecular operational taxonomic units (MOTU) based on barcode divergences using the RESL algorithm (Ratnasingham & Hebert, 2013). In addition to DNA barcode derived taxon richness estimators, I calculated phylogenetic diversity of the staphylinids by constructing a maximum likelihood tree in MEGA5 using a single-representative sequence for each species (Tamura et al., 2013). The best substitution models to describe the substitution pattern were calculated in MEGA5 (Nei & Kumar, 2000; Tamura et al., 2013). The ML tree was created using a general time reversible model with discrete gamma distribution (GTR + G) (Nei & Kumar, 2000; Tamura et al., 2013). Subsequent calculations of the summation of branch lengths within a community (phylogenetic diversity) were made using the picante package (Kembel et al., 2010) in R (R Core Team, 2013).

I used rarefaction and non-parametric estimators to measure sampling intensity to predict diversity and evaluate sampling variation amongst sites (Smith et al., 2009). I used observed species estimators (derived from BIN estimates) run 1000 times to calculate observed species (CHAO 1 Mean (Chao, 1987), Mao Tau, ICE mean, and Jack 1 Mean (Colwell et al., 2012) at each site.

2.2.6 Beta Diversity

To calculate betadiversity, I used a pair-wise Jaccard Index (Jaccard, 1901). The Jaccard Index determines the percent similarity of each elevation site by examining the number of shared BINs between each site. I additionally used a Mantel test (Mantel, 1967) in R (R Core Team, 2013) using the package *ade4* with 1000 replications to determine if distances between elevation sites were related to BIN-based Jaccard Classic values.

I further tested the nature of the beta diversity patterns by testing whether the species shared between sites is a result of nestedness (species from one community are nested within other communities) or turnover (distinct communities across gradient with limited species shared between sites) using the package *betapart* (Baselga, 2010; Baselga & Orme, 2012) in R Studio.

2.2.7 Phylogenetic Community Structure

To examine phylogenetic community structure, I made an incidence matrix of BINs and sites, and used the maximum likelihood phylogeny described above. The community data matrix was first randomized to determine a random phylogenetic distance in order to compare the calculated observed values to (mean distance (taxalabels)). I randomized the matrix using the “taxalabels” null model to maintain species richness and frequency within a sample site (Gotelli & Graves, 1996). Though the gradient is relatively small, the abiotic conditions change drastically. I therefore reasoned that while there was a low chance of species being equally present in all communities, it was still possible, so I tested both the “taxa.labels” and “independentswap” null models as suggested by (Gotelli & Graves, 1996).

Taxon richness and the mean nearest taxon distance (MNTD) (distance observed) was calculated using the *ses.mntd* function in the *picante* package (Kembel et al., 2010) in R (R Core Team, 2013). I used the nearest taxon index (NTI), $(-1[\frac{\text{distance observed} - \text{mean distance (independentswap)}}{\text{standard deviation}}])$, from this output for all further analyses. NTI (the

mean taxon distance within a site) was chosen because it is a standardized measure of the phylogenetic distance to the nearest taxon, and since it is a measure of terminal clustering independent of deep level clustering, it is most appropriate for phylogenetic estimates derived from DNA barcodes (Smith, Hallwachs & Janzen, 2014). I considered observed outputs of $p < 0.05$ to indicate phylogenetic clustering.

Additionally, I completed the analyses described above but used forest type (dry, rain, or cloud) rather than specific elevation. To do so, I remade the incidence matrices and combined all sites within one distinct forest type. I considered sites from sea level to 600 m to be dry forest, sites from 700 – 1200 m to be rain forest and sites above 1300 m to be cloud forest (Fig. 1).

2.2.8 Comparing diversity and abundance to abiotic explanatory variables

To test the relationship between staphylinid abundance, BIN richness, and phylogenetic diversity against independent variables of area, elevation, precipitation, and temperature. I performed general linear regressions in R (R Core Team, 2013). I also used a general linear regression of the log of both MOTU richness and surface area to better fit the normality of residuals. I further examined the residuals of the relationship between PD and MOTU richness to determine if there were elevational sites where PD was higher or lower than was predicted by MOTU richness.

I additionally used a multiple linear regression to test the relationship between staphylinid BIN richness against independent variables of area, elevation, precipitation, and temperature. Due to the collinearity between these variables as is expected along a gradient, I used a stepwise regression to determine which variables should be included in the regression model. The stepwise regression excluded elevation, and so my final model contained the independent variables of $\log(\text{area})$, precipitation, and temperature. Surface area was transformed using a log equation because this way it better fit the normality of residuals assumption. Abundance was included in the model in a separate analysis. The same model was used to test the relationship to nearest taxon index. All analyses were performed in R using the package “MASS” for the stepwise regression (R Core Team, 2013).

To determine if there was a mid-elevation peak (or trough) of MOTU richness or NTI, I tested the fit of our data to a second order quadratic function (based on Akaike information criterion (AIC (Akaike, 1973))).

To test if patterns at a family level differ across other taxonomic levels, analysis of MOTU richness, PD, and NTI were estimated within the largest 3 subfamilies. I then additionally tested the same statistics within the 3 most abundant subfamilies.

2.3 Results

2.3.1 Alpha Diversity

Two-thousand six hundred and one (2,601) staphylinids were collected between 2008 and 2017 on Volcan Cacao. Staphylinid abundance was positively, linearly, and significantly related to elevation ($df = 7$, $F = 14.1$, $R^2 = 0.701$, $p < 0.01$; Fig 2a).

From all beetle collections, 2,120 (81%) were successfully barcoded. Using these barcodes to generate BINs as species proxies, I found 369 BINs across the elevation gradient and this diversity was positively, linearly, and significantly related to elevation ($df = 7$, $F = 63.3$, $R^2 = 0.913$, $p < 0.01$; Fig 2c). As with most studies of neotropical invertebrates (Novotný & Basset, 2000), this collection was dominated by singletons and doubletons; (52% (195) of these BINs were collected only once, and 70% (258) of the total BINs were present at only one site (i.e. elevation)) (Fig 3).

Whether diversity was calculated using BINs or phylogenetic diversity, it was positively and linearly related to elevation. BIN richness displayed a positive, linear, and significant relationship with elevation ($df = 7$, $F = 62.7$, $R^2 = 0.912$, $p < 0.001$; Fig 2c), and was not well described using a quadratic (order 2) function ($df = 5$, $F = 26.2$, $R^2 = 0.878$, $p = 0.884$). Phylogenetic diversity was also positively related to elevation ($df = 7$, $F = 135$, $R^2 = 0.957$, $p < 0.001$; Fig 2d). Phylogenetic diversity and BIN richness were positively and linearly related ($df = 7$, $F = 665$, $R^2 = 0.991$, $p < 0.001$; Fig 4).

Log(MOTU Richness) was negatively related to log(Surface Area) ($df = 6$, $F = 10.4$, $R^2 = 0.676$, $p = 0.023$; Fig 5A). MOTU richness was negatively related to average daily temperature ($df = 7$, $F = 47.2$, $R^2 = 0.887$, $p < 0.001$), minimum daily temperature ($df = 7$, $F = 55.4$, $R^2 = 0.902$, $p < 0.001$), and maximum daily temperature ($df = 7$, $F = 40.2$, $R^2 = 0.870$, $p < 0.001$; Fig 5C). MOTU richness was positively related to average annual precipitation ($df = 7$, $F = 13.1$, $R^2 = 0.686$, $p = 0.011$; Fig 5E).

Using a multiple linear regression, BIN richness was positively and linearly related to the abiotic factors that covary with elevation using maximum daily temperature, log surface area, and mean annual precipitation in the model ($df = 7$, $F = 37.9$, $p = 0.002$). Within the model maximum daily temperature and mean annual precipitation were significant ($p = 0.004$ and $p = 0.038$), while log surface area was moderately significant ($p = 0.095$). When abundance is included as a covariate in the model, the relationship is significant ($df = 7$, $F = 75.6$, $p = 0.002$), but within the model abundance is not a significant factor influencing richness ($p = 0.067$).

Estimates of species accumulation using CHAO 1 Mean (Chao, 1987), Mao Tau, ICE mean, and Jack 1 Mean (Colwell et al., 2012) shows an asymptotic relationship at 300 m, 1200 m, and 1500 m between the number of MOTUs and the number of sampling events at any of the 8 elevation sites (Fig S2).

2.3.2 Subfamily Alpha Diversity

A total of 17 different subfamilies were identified within the collected Staphylinids. The largest 3 subfamilies were Aleocharinae ($n = 1,202$), Oxytelinae ($n = 207$), and Scydmaeninae ($n = 181$). Aleocharinae MOTU richness was positively related to elevation ($df = 7$, $F = 23.44$, $R^2 = 0.796$, $p = 0.003$; Fig 6A). Oxytelinae MOTU richness was not related to elevation linearly ($df = 7$, $F = 4.14$, $p = 0.088$; Fig 6C). Scydmaeninae MOTU richness was positively related to elevation ($df = 7$, $F = 26.4$, $R^2 = 0.815$, $p = 0.002$; Fig 6E).

2.3.3 Beta Diversity

Jaccard Classic values of shared BINs between sites were low overall (mean = 0.081). The distance between elevation site was related to BIN-based Jaccard Classic values ($r = 0.734$, $p = 0.004$; Fig 7). Betapart analysis of turnover and nestedness index demonstrated that staphylinid communities are distinct elevation band communities (high species turnover amongst sites), as opposed to the diversity being nested within other sites (Simpson dissimilarity = 0.822, Sorenson dissimilarity = 0.073; Fig S3).

2.3.4 Phylogenetic Community Structure

Patterns observed using null models of “taxa.labels” and “independentswap” were similar, and so for simplicity I present the findings from “taxa.labels”. Staphylinid community NTI displayed neither a linear relation ($df = 7$, $F = 1.2$, $R^2 = 0.166$, $p = 0.315$; Fig 8) nor a mid-

elevation trough ($df = 5$, $F = 1.32$, $R^2 = 0.345$, $p = 0.347$; Fig 8). However, significant phylogenetic clustering was evident at 300 m ($NTI = 2.38$, $p = 0.012$), 1200 m ($NTI = 1.73$, $p = 0.047$), and 1300 m ($NTI = 1.76$, $p = 0.043$).

NTI was not linearly related to the climatic factors that co-vary with elevation, including area ($df = 7$, $F = 1.78$, $R^2 = 0.229$, $p = 0.230$; Fig 5B), maximum daily temperature ($df = 7$, $F = 0.977$, $R^2 = 0.140$, $p = 0.361$; Fig 5D), or average annual precipitation ($df = 7$, $F = 1.78$, $R^2 = 0.229$, $p = 0.230$; Fig 5E). NTI was additionally not linearly related to the climatic factors that co-vary with elevation using a multiple linear regression ($df = 4$, $F = 1.45$, $p = 0.355$).

2.3.5 Subfamily Phylogenetic Community Structure

Aleocharinae NTI across the gradient did not have a mid-elevation trough (Fig 6B). Aleocharinae community at 1300 m was significantly phylogenetically clustered ($NTI = 2.75$, $p = 0.004$). Oxyelinae NTI across the gradient showed no pattern (Fig 6D). NTI of Scydmaeninae was negatively related to elevation from 600 m to 1500 m ($df = 5$, $F = 9.70$, $R^2 = 0.708$, $p = 0.036$; Fig 6E).

2.4 Discussion

A decade of sampling yielded 2,601 staphylinids across an elevation gradient in the ACG. I found that staphylinid MOTU and phylogenetic diversity are related to elevation and the climatic factors that co-vary with elevation. ACG staphylinid diversity also showed a strong and significant species-area trend – but in the opposite direction to what I had predicted as diversity increased with decreasing area. Amongst elevational sites there was high species turnover. My results suggest these high elevation montane cloud forests are not imposing environmental stress on inhabitants, but instead seem to act as refugia for staphylinids. These high elevations may be the last existing areas of the environment where they flourish, and perhaps provides insight into what staphylinid diversity looked like across the gradient at the last glacial maxima.

Contrary to my prediction that stressful abiotic conditions in the cloud forest at the peak of this gradient would impose environmental stress on inhabitants and decrease their diversity, I found that cold wet high elevation environments had the highest diversity (measured phylogenetically or via BINs). Diversity was also significantly related to the abiotic factors that co-vary with elevation such as average daily precipitation (positive) and temperature (negative). This pattern not only contradicts other studies of staphylinid richness with elevation (mid

elevation- Staunton et al. (2011) and Paill & Kahlen (2009) in Betz, Irmiler & Klimaszewski, (2018)), but also most other richness and elevation studies. A meta-analysis of species richness patterns with elevation by McCain & Grytness (2010) identified the four main patterns of richness as elevation increases: richness decreases, mid elevation peak, low elevation plateau in richness, and low elevation plateau with a mid-elevation peak. Instances of increased richness with increasing elevation are rare. In the literature, I am aware of a small number of examples including (family) beetles (Odegaard & Diserud, 2011), a subfamily of Andean geometrid moths (Brehm, Süssenbach & Fiedler, 2003), some mesoAmerican species of (Wake & Papenfuss, 1992), lichen (Martin & Arbor, 1958), and bacteria (Wang et al., 2011). Despite these all being organisms that cannot produce their own heat, they are increasing in diversity in colder environments – making this a novel finding.

Surface area across the gradient was related to staphylinid diversity in the opposite direction to what the species-area hypothesis predicted. This may indicate that historical, rather than contemporary estimates of habitat area best explain the species-area relationship. Consider that, following the colonization of these volcanic slopes by forest, it is thought that they experienced a period of pronounced cooling during the Pleistocene (Janzen, 1983). During this time, it is estimated that in northwestern Costa Rica the cloud forest extended from the tips to the bases of these volcanoes (Ramírez-Barahona & Eguiarte, 2013), and so cloud forest, rather than being the isolated “sky islands” of habitat we see today, would have covered much of the area protected within the ACG. As climate warmed, larger and more connected cloud forests became small and (vertically and horizontally) isolated islands (Ramírez-Barahona & Eguiarte, 2014). Climate change occurs more rapidly than trait adaptation to climate change, so with this retreat, staphylinid diversity may also have withdrawn to the tips of the volcanoes (Ramírez-Barahona & Eguiarte, 2013). I therefore suggest that the pattern we see in this contemporary habitat, is not driven by contemporary ecological limitations, but is rather a legacy of a historical biogeographical species-area relationship.

Phylogenetic diversity and MOTU diversity were linearly related. The largest departure from this pattern was notably at 1500 m. Here, the phylogenetic diversity observed was much higher than predicted by MOTU richness (Zou et al., 2016). Through analysis of phylogenetic community structure, I found that the 1500 m site was the only site to be slightly phylogenetically dispersed, consistent with our findings of this site being slightly more phylogenetically diverse than is predicted by species richness at this site. The high phylogenetic diversity and tight

relationship to the climatic factors in the cloud forest suggests that these patterns may be driven by historical patterns of biogeography rather than environmental stress, since higher phylogenetic diversity suggests more evolutionary history.

Alternatively, a pattern of higher diversity in the cloud forests may be a result of local ecological change that is driving selection in these environments. García-París et al. (1998) hypothesized that local ecological gradients, such as smaller changes in abiotic conditions within sites, drives local selection amongst continuously distributed populations. According to this model, environmental and habitat heterogeneity in the cloud forest facilitates species formation. Although intuitively appealing, the paucity of examples in the literature of increasing diversity with elevation suggests that this potential mechanism may not frequently affect elevational diversity gradients (Rahbek, 1995; McCain & Grytness, 2010).

One way to differentiate the mechanisms of this richness pattern would be to extend my phylogenetic analysis beyond the mitochondria to a multi-gene phylogeny. If cloud forests are supporting local speciation via the fragmentation and extreme niche segregation (as a cradle for evolution) predicted by García-París et al. (1998), I would expect that species in high elevation cloud forests to have shorter branch lengths (and higher species: genus ratio) than lower elevation forests. Alternatively, if high elevations serve as a type of museum for staphylinids, than I would expect individuals here to have more deeply rooted species (and lower species: genus ratio). For example, Moreau & Bell (2013) was able to investigate these hypotheses in Neotropical ant assemblages using a well-resolved tree. They found that the Neotropics acted as both a museum and cradle for diversity, where there is evidence of historical and more recent diversification events (Moreau & Bell, 2013). Therefore, it is possible that the high elevation staphylinid communities are acting as a museum for staphylinid traits but also developing them. This finding would not be unique to staphylinids, because it has been found in numerous taxa in the Neotropics (See examples in Moreau & Bell (2013)).

Richness patterns across elevation gradients are often used as surrogates for trends seen across larger latitudinal gradients (McCain & Grytness, 2010), so if elevation gradients are analogous to latitudinal gradients, is the same anomalous pattern evident as latitude increases? I assembled a rapid test of this by assembling all current publically accessible staphylinid records on BOLD (Accessed 18-06-01, total records = 56,501, total BINS = 4,051; http://v3.boldsystems.org/index.php/API_Public/combined?taxon=Staphylinidae&format=xml). Across latitudinal categories of 5°, from 0° - 75° N, BIN richness peaks at latitudes between

45° and 55° N and does not increase linearly with latitude (Fig S3). BIN richness also peaks at mean annual temperatures of 5 - 6 °C and mean annual precipitation of 600 – 800 mm. This synthesis of data from BOLD is evidently affected by the differences in sample sizes across this gradient, but regardless, richness does not consistently increase with decreasing temperature and increasing precipitation like I found with the ACG staphylinids. The highest elevation sites in the ACG are cold and wet, but it is still a tropical environment and so these cold sites still have an average daily temperature of 17°C. The highest elevation sites in the ACG may be representing their ideal niche as cool and wet, if these temperatures dropped lower, we may see a trend like Heino, Alahuhta & Fattorini (2015) who found a positive correlation between beetle richness and maximum temperature in Northern Europe, a study site that would represent much lower temperatures than would be found in the ACG. Another example is the staphylinid richness mid-elevation peak found in Röder et al. (2017), where the mid-elevation climatic conditions would represent conditions found at the high elevation sites in the ACG. So, if I extend my argument back to the elevational gradient examined here, my results may show that more localized environmental factors are driving richness patterns of staphylinids in the ACG.

The collections of staphylinids across this elevational gradient were dominated by singletons and species with (evidently) elevation restricted distributions. Seventy percent of the MOTUs I characterized were present at only 1 elevation site, and 53% of the total MOTUs were single specimens (singletons). High species turnover observed here does not support the theory from island biogeography that the larger area act as a source population to smaller insular environments, and that closer islands should be more similar to each other than more distant islands (MacArthur & Wilson, 1967). This pattern of high species turnover amongst elevation communities is consistent with staphylinid literature. For example, Gutiérrez-Chacón & Ulloa-Chacón (2006) found nearly the same percentage of singletons across an elevational gradient in Colombia. Most of the taxa studied to date across this particular elevational gradient also demonstrate such high turnover including ants, spiders, springtails, isopods, and parasitoid wasps (Smith et al., 2015). Such results support the Janzen (1967) hypothesis regarding the comparatively greater zonation along tropical elevation gradients compared to temperate gradients. These tropical distinct elevation bands further suggest the vulnerability of this ecosystem (Smith, Hallwachs & Janzen, 2014). Climate change in the neotropics threatens to alter these systems including upward shifts in dryer elevation climate bands, and possible high elevation habitat extinction due to no possible migration upwards (Colwell et al., 2008). High diversity in the cloud forest and high habitat specialization across the entire gradient suggests

the disruption and possible elimination of habitats, and staphylinid communities, in the face of oncoming climate drying (Smith, Hallwachs & Janzen, 2014).

Staphylinid phylogenetic community structure was somewhat related to elevation and the environmental factors that co-vary with elevation. Evidence of significant phylogenetic clustering was found at the low elevation (dry forest) site 300 m, and the high elevation sites 1200 m, and 1300 m (cloud forest). While I found greater statistically significant support for phylogenetic clustering at the scale of specific elevational collection sites (rather than the forest type scale), the overall pattern of community structure across the forest type scale more closely resembled my predictions (clustering (and thus perhaps evidence of stress and filtering) at high and low elevations). Consistent with my predictions, environmentally stressful dry forest (low elevation) and cloud forest (high elevation) communities were more phylogenetically clustered than rain forests (mid elevation). As predicted, hot dry forests may then be imposing environmental stress for organisms needing moisture, while cold and wet cloud forests may be imposing environmental stress for organisms needing higher temperatures, and thus resulting in filtering of the taxonomic tree, resulting in specific clades persisting in these environments. The clear next step would be to test for the presence of a trait or traits that enable their presence here.

Some research has suggested that ant diversity is an indicator of staphylinid diversity due to the close association between ants and some staphylinid groups (Pselaphine, specifically) (Psomas, Holdsworth & Eggleton, 2018). Across the same gradient, Smith, Hallwachs & Janzen (2014) found that ant diversity peaked at mid-elevations, and high elevation communities were phylogenetically clustered. These standardized collections did not include the pselaphines but did include Scydmaeninae which are also frequently associated with ants (Psomas, Holdsworth & Eggleton, 2018). Similar to the total staphylinid diversity, and not like the ants, scydmaenins showed an increase in species richness with increased elevation. However, NTI of the scydmaenins across elevation significantly decreases from phylogenetic evenness to a mild signal of phylogenetic overdispersion. There is only 1 MOTU at the 10 m and 300 m sites and therefore this group was only recorded from 600 m onwards. This pattern contradicts my initial predictions, the patterns seen across all of staphylinids, and patterns seen in the ants. Not all subfamilies that I tested responded the same to elevation and the factors that co-vary with elevation. Aleocharinae MOTU richness was positively related to elevation, and the same seen across the rest of staphylinids, However NTI of Aleocharinae differs from that of all of staphylinidae and more clearly displays the patterns I predicted. The opposite trends seen in

Scydmaeninae in comparison to Aleocharinae or all of Staphylinidae indicates that patterns at lower taxonomic scales do not mimic what is seen at the family level. Opposing trends such as this in response to elevation at lower taxonomic scales may thus be the reason for no clear trends at the family level.

In this documentation of staphylinids in the neotropics, I found that staphylinids are most abundant and diverse in one of the most vulnerable habitats (tropical montane cloud forests). I further hypothesized that this diversity at the tips of these volcanoes may be acting as a repository or museum for species traits. Future research should focus on the drivers of phylogenetic diversity here to better understand these communities and how they may change in the face of climate change. Other descriptive studies should be conducted in other locations and using other taxa in order to have a more thorough understanding of what factors and how these factors drive biodiversity as a whole. This categorization of diversity and its relationships to climate is critical in the preservation and maintenance of biodiversity.

CHAPTER 3: Epilogue

I found an anomalous pattern of diversity and elevation within a set of neotropical staphylinids. Contrary to my expectation and prediction that diversity would peak at mid-elevations, staphylinid species richness and phylogenetic diversity increased with increasing elevation in the ACG. Contemporary abiotic factors of temperature, precipitation, and area were significantly related to these patterns. One explanation may be that the highest elevation sites have the largest evolutionary history and diversity captured. This result makes sense given the historical biogeographical trends within the ACG during the last glacial maxima where cloud forests likely extended downslope across much more of the ACG elevation gradient. The high diversity that I document here at the tops of these mountains may be the remaining lineages and diversity from these ice ages, which have shrunk to encompass the smallest areas on the gradient, resulting in the high phylogenetic diversity seen. Alternatively, it is possible that the high habitat and environmental heterogeneity in the cloud forest is driving local selection here (García-París et al., 1998).

Regardless of the mechanisms behind it, increased species richness with elevation is a novel finding. It is clear through other studies of taxa in the ACG (Smith, Hallwachs & Janzen, 2014; Smith et al., 2015), and elsewhere (Staunton et al., 2011), that few organisms respond in the same way to the same environmental factors. Thus, while this study aids in the documentation and understanding of staphylinids in the ACG, it should not be read as a prediction about the trends that other taxa will exhibit, and more taxa should be investigated to better understand the factors affecting arthropod communities. Additionally, more natural history information, such as functional traits enabling staphylinid persistence in the cloud forest, would benefit our understanding of these systems (example: Hansen et al., 2018).

High species richness and high phylogenetic diversity support the notion that these tropical montane cloud forests serve as a type of museum or repository for species and possibly for traits. These environments, however, are the most vulnerable to the drying and warming with oncoming climate change (Mora et al., 2013). The loss of these environments threatens to eliminate arthropod populations and can have severe effects on surrounding communities and the taxa that rely on them. My work has shown that one of the most diverse families of animals in the world is extremely abundant and diverse in one of the most vulnerable habitats. This work

has thus demonstrated that understanding and conserving these environments is critical to the preservation and maintenance of biodiversity – more critical than we had previously realized.

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Figures

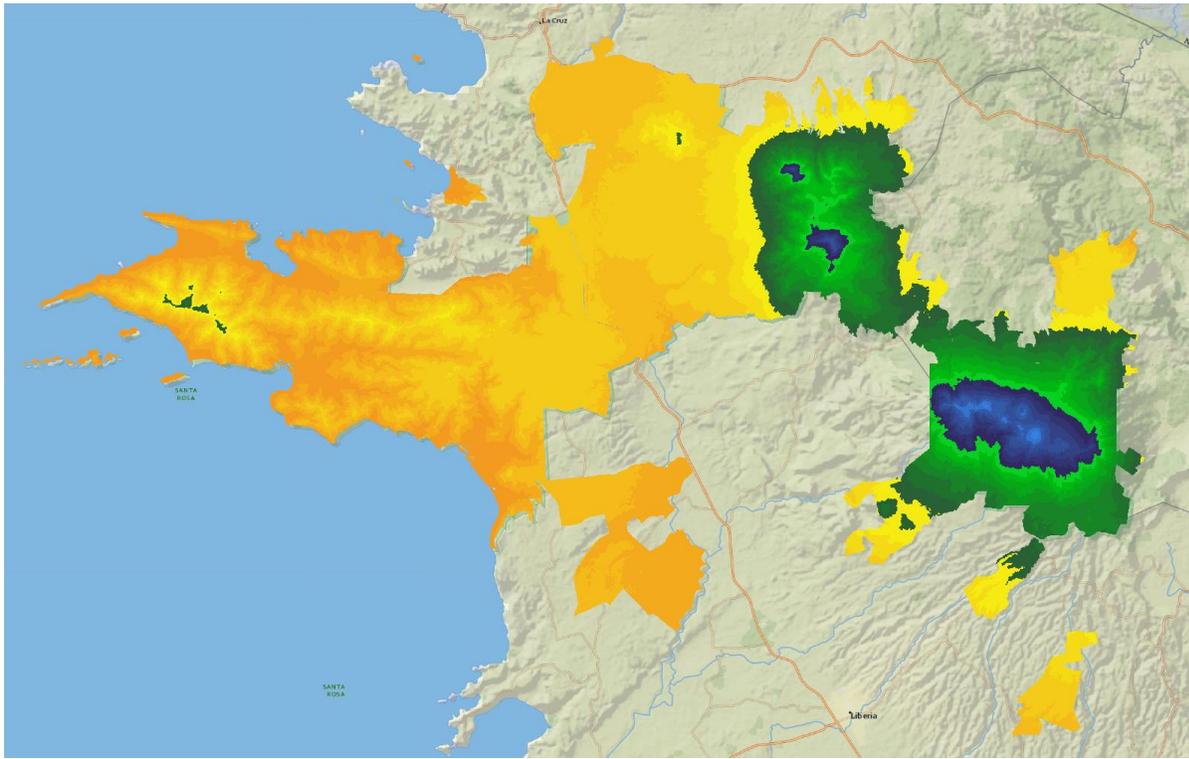


Figure 1: Map of the protected areas of the Area de Conservación Guanacaste in Costa Rica. Color changes from yellow, green, and blue represent general changes in elevation (and more generally, forest type); yellow: 10 – 600 m (~low elevation dry forest), green: 700 – 1200 m (~mid elevation rain forest), blue: 1300 – 1500 m (~ high elevation tropical montane cloud forest). Each shade change within the colored forest types represents a 100 m change in elevation (darkest colors are lowest elevation). Elevational bands were calculated using EOSDIS data and extracted in ArcGIS (<https://earthdata.nasa.gov/>; <http://www.esri.com>).

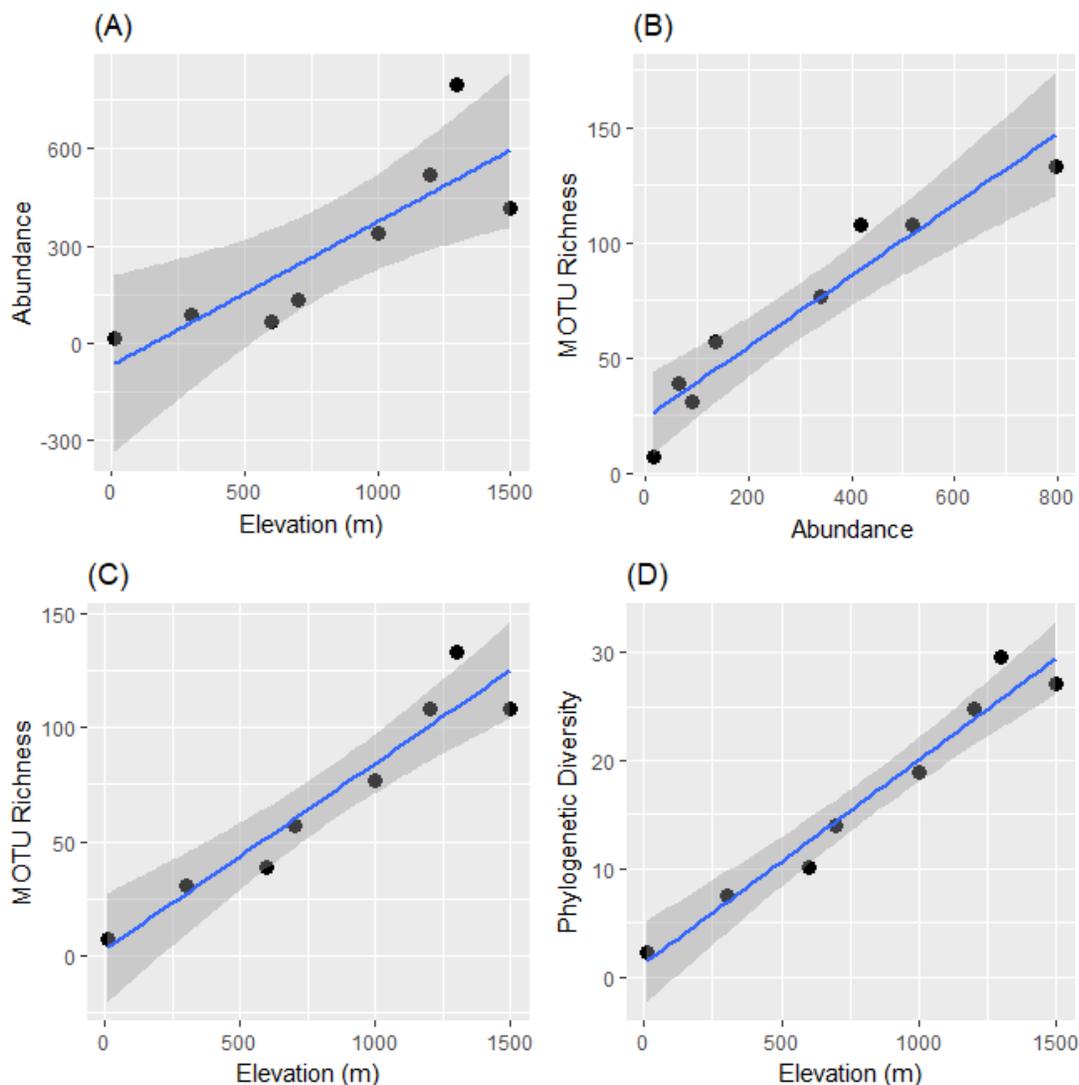


Figure 2: The relationship between staphylinid richness, abundance, and elevation. (A) Staphylinid abundance is positively related to elevation across the 1500 m elevation gradient in the ACG. (B) Staphylinid MOTU richness is positively related to staphylinid abundance. (C) MOTU richness of staphylinids is positively related with elevation. (D) Phylogenetic diversity increases as elevation increases for staphylinid communities in the ACG.

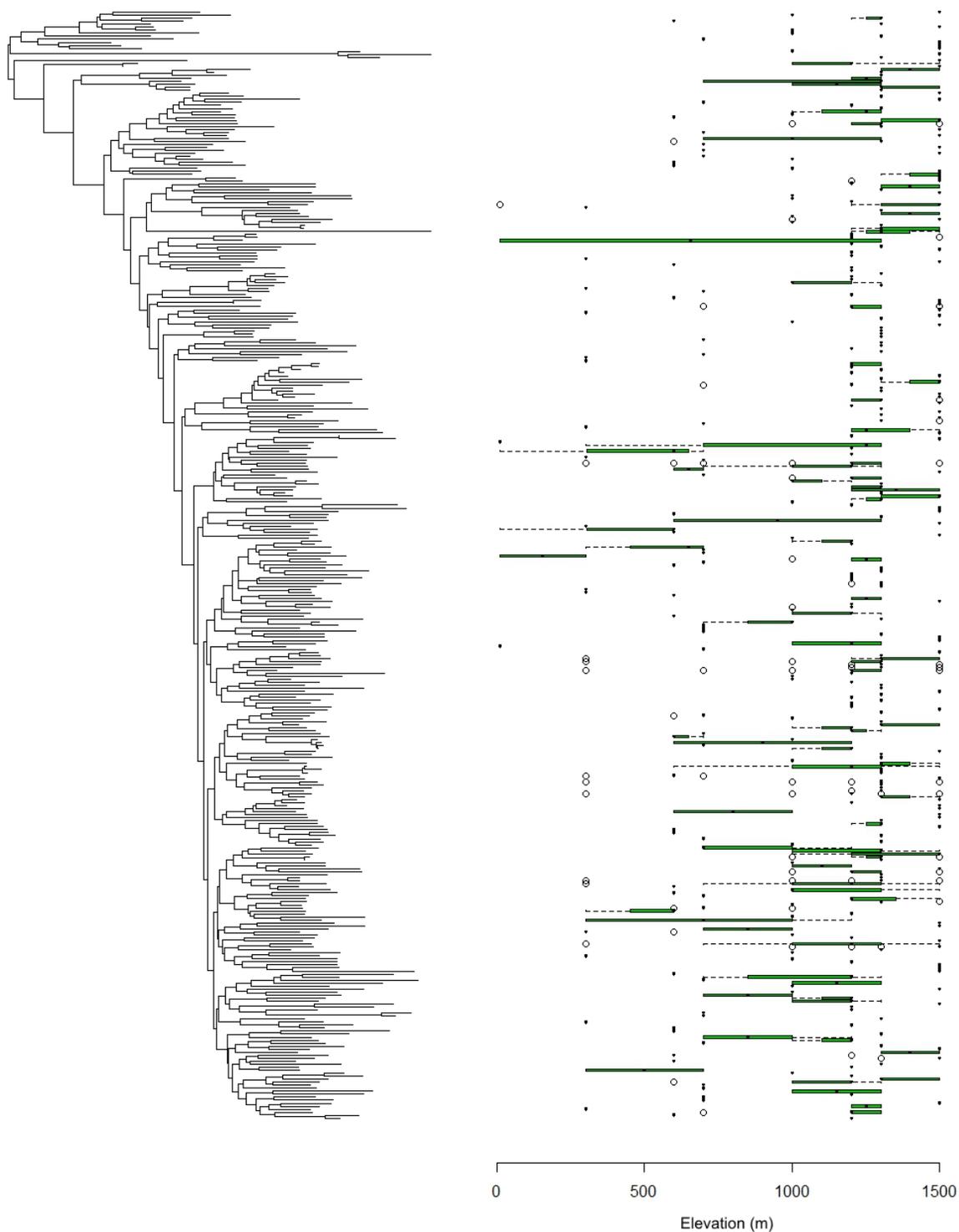


Figure 3: Single-representative Maximum likelihood tree of 369 staphylinid MOTUs in the ACG. This tree was created in MEGA6 using a GTR + G substitution model and the boxplot represents the 95% confidence interval of the elevational distribution for each corresponding MOTUs. Solid

black dots represent MOTUs only present at one elevation site. Hollow circles indicate outliers; lines within boxplots indicate the mean.

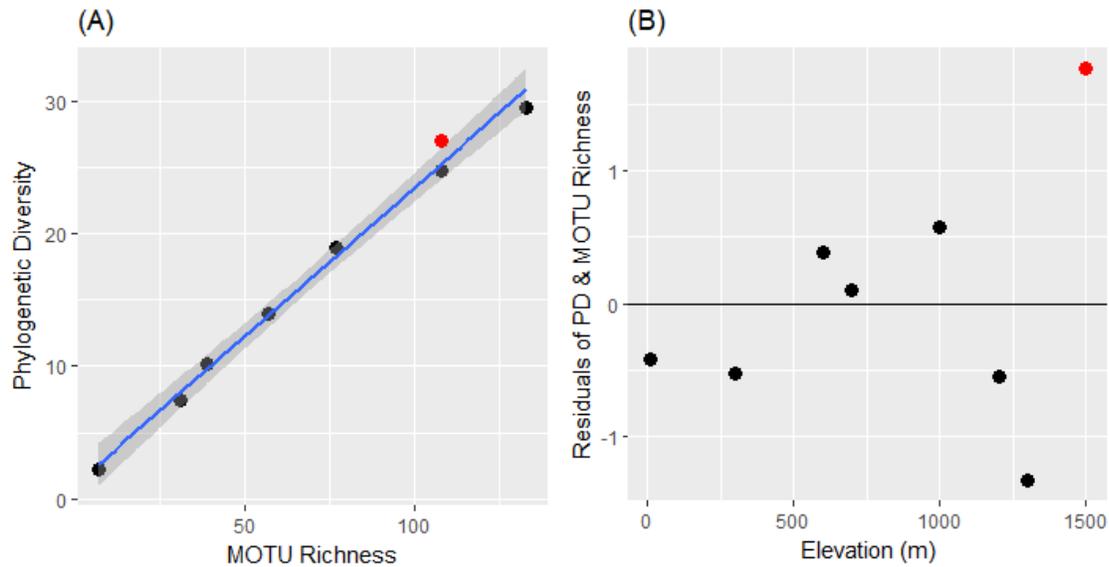


Figure 4: (A) Phylogenetic diversity (PD) and species richness are positively related. The linear trend line is demonstrating a significant relationship. The 1500 m site is indicated by a red point and notes the only site with higher phylogenetic diversity than should be predicted with MOTU richness. (B) The relationship between the residuals of phylogenetic diversity and MOTU richness with elevation. The proportionally high phylogenetic diversity at 1500 m can also be seen here in red.

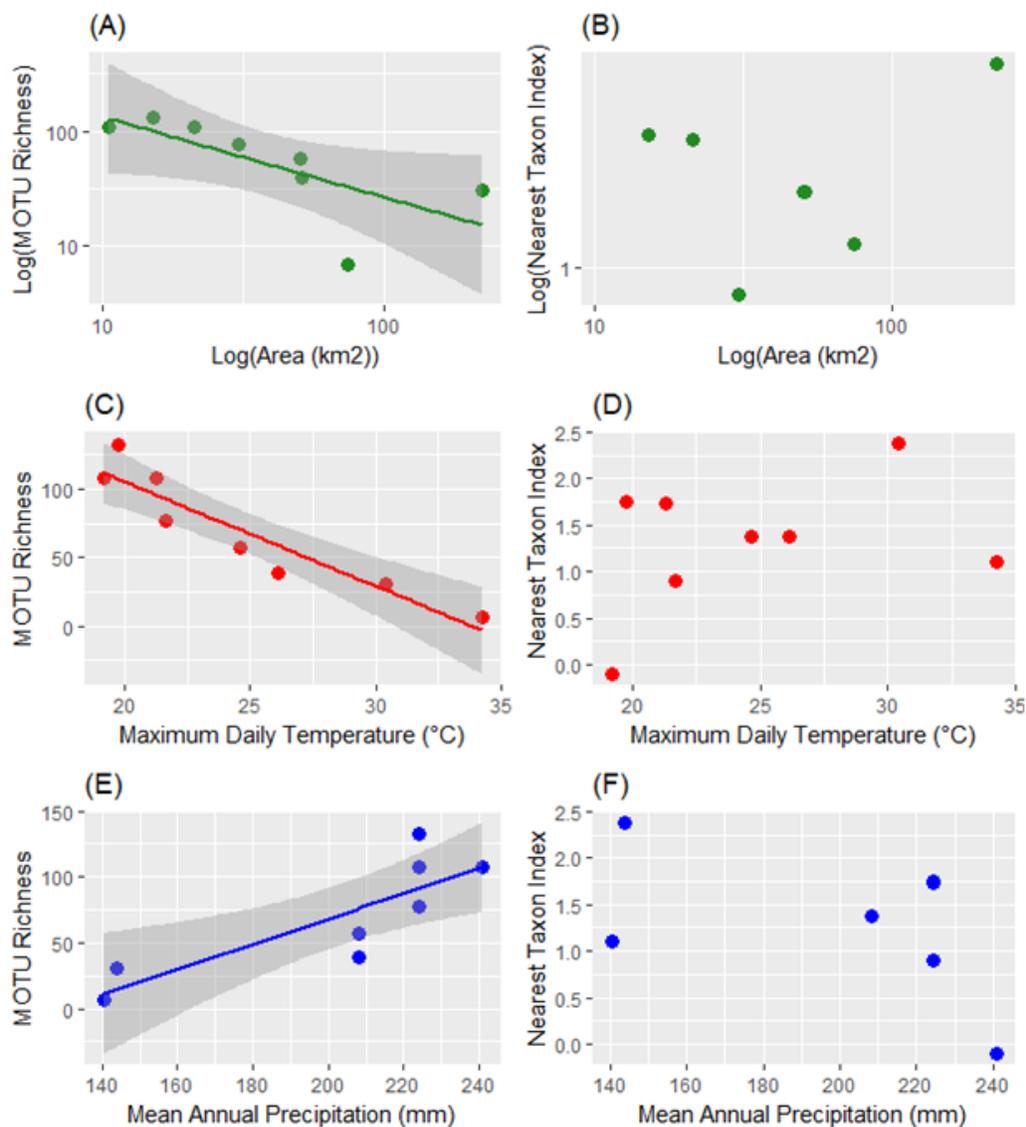


Figure 5: MOTU richness of staphylinids is (A) negatively related to the amount of surface area at each elevation in the ACG, (C) negatively related to the maximum daily temperature, (E) positively related to mean annual precipitation. Nearest Taxon Index of staphylinid communities is not related to (B) surface area (D) maximum daily temperature, (F) mean annual precipitation. Linear trend lines shown only where there was a significant linear relationship.

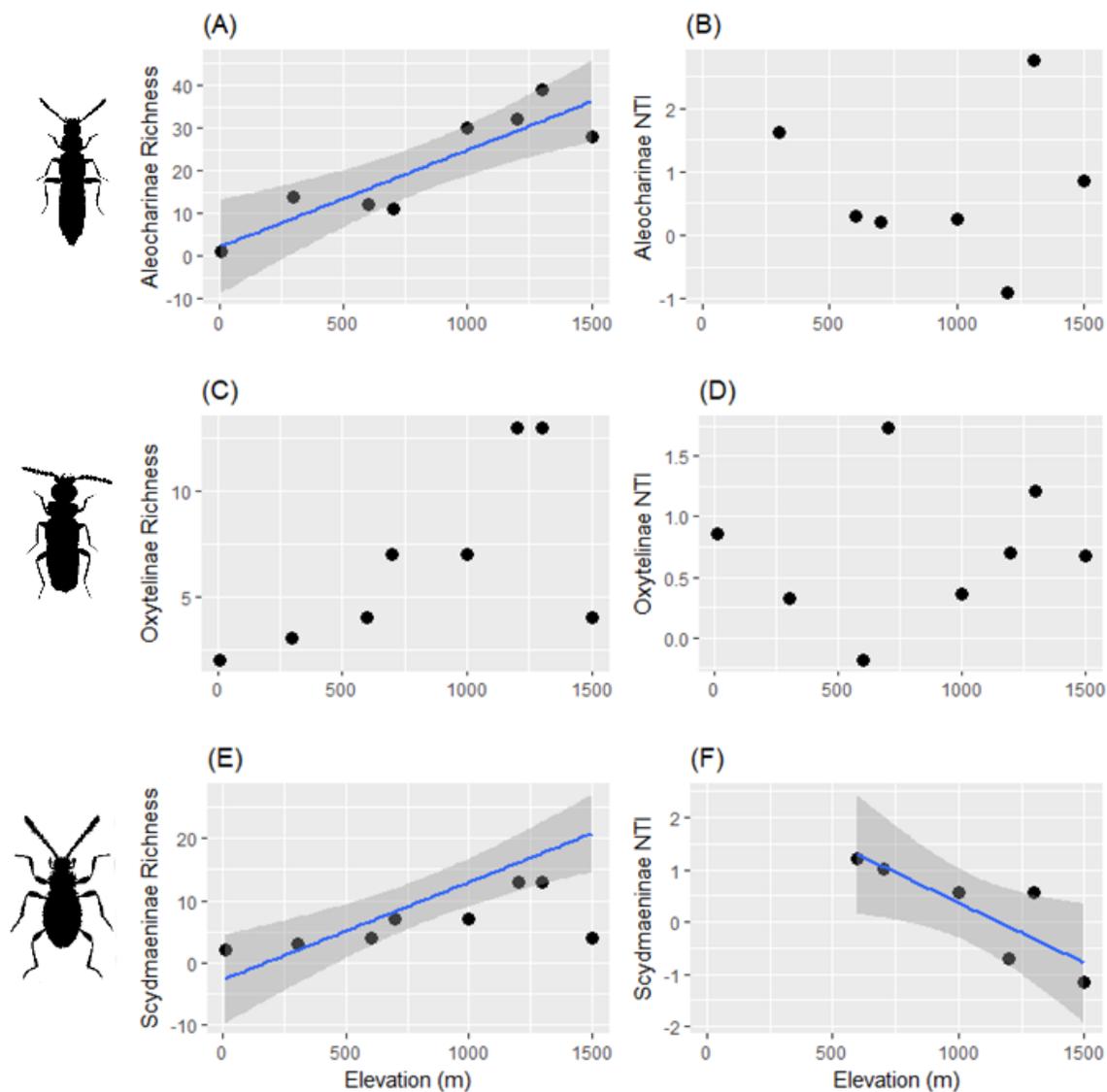


Figure 6: MOTU richness across the elevation gradient of (A) Aleocharinae, (C) Oxytelinae, and (E) Scydmaeninae. Nearest taxon index of (B) Aleocharinae, (D) Oxytelinae, and (F) Scydmaeninae. Linear trend lines only shown on graphs that had a significant linear relationship. Scydmaenines only had more than 1 MOTU from 600 m and lower and thus NTI values are not possible to calculate beneath 600 m.

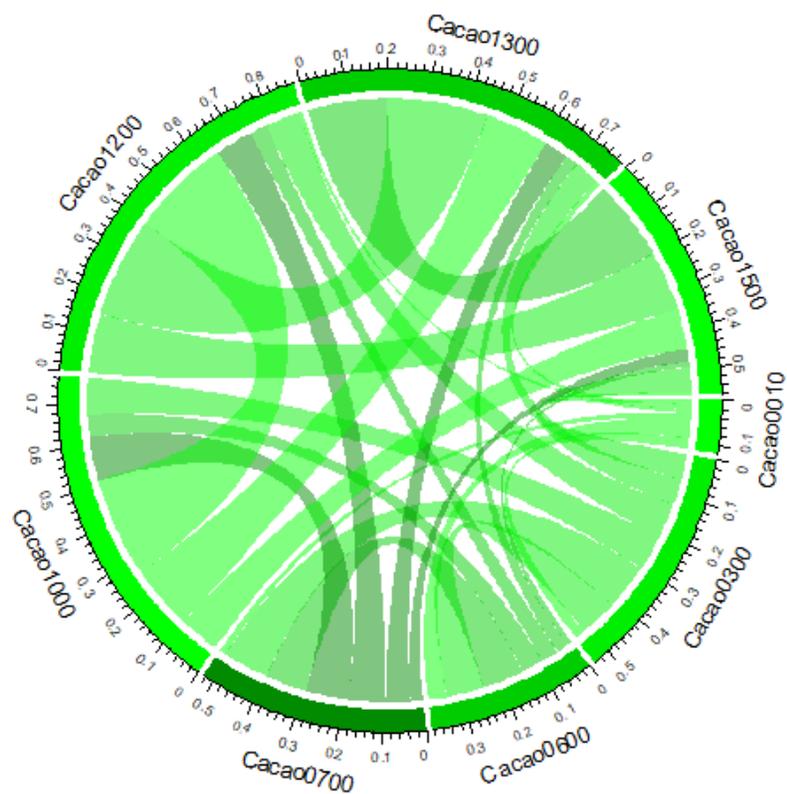


Figure 7: Chord diagram showing the proportion of shared species between each elevation community of staphylinids (beta diversity). Proportions calculated and displayed here through Jaccard score.

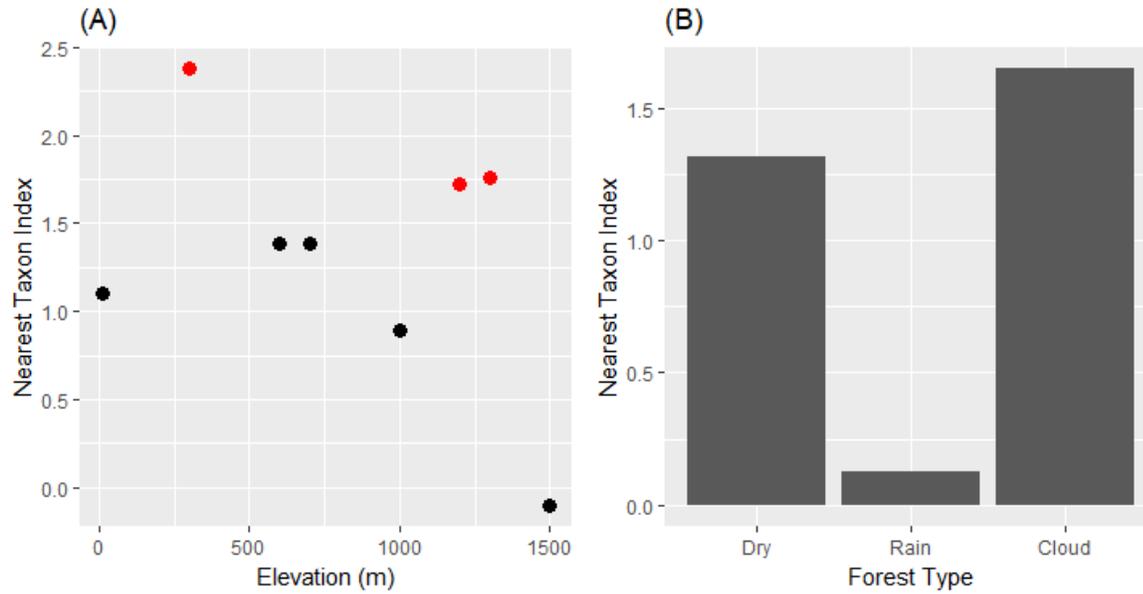


Figure 8: Nearest taxon index of staphylinid communities in the ACG. (A) No significant pattern was observed continuously across elevation. Sites that were significantly phylogenetically clustered are represented in red. The 1500 m elevation site is the only site with a negative NTI value. (B) Clear pattern of NTI across the gradient when grouped in forest types. Low elevations are dry forests, mid elevations are rain forests, and high elevations are tropical montane cloud forests.

Appendix 1

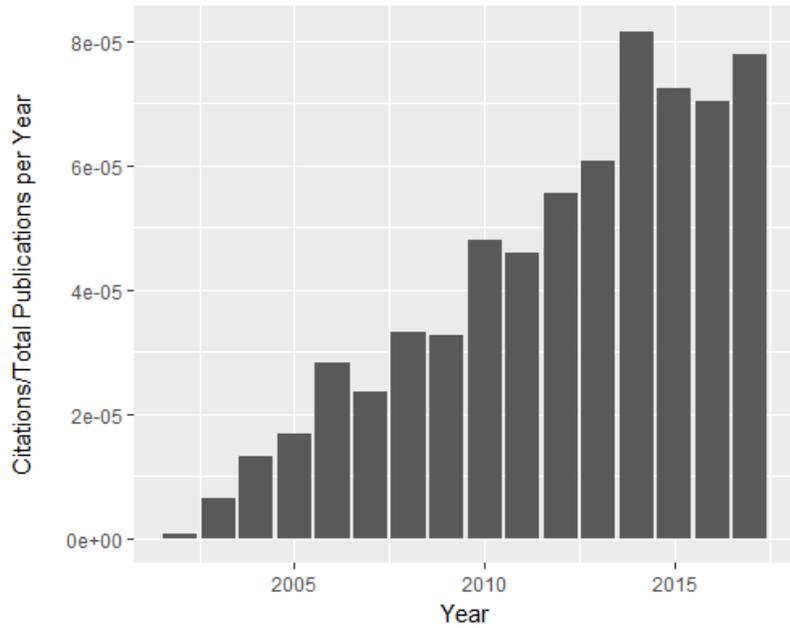


Figure S1. Citation report for Webb (2002) demonstrating the use of phylogenetic community structure in manuscripts measured through citations per year. Data downloaded from Web of Science.

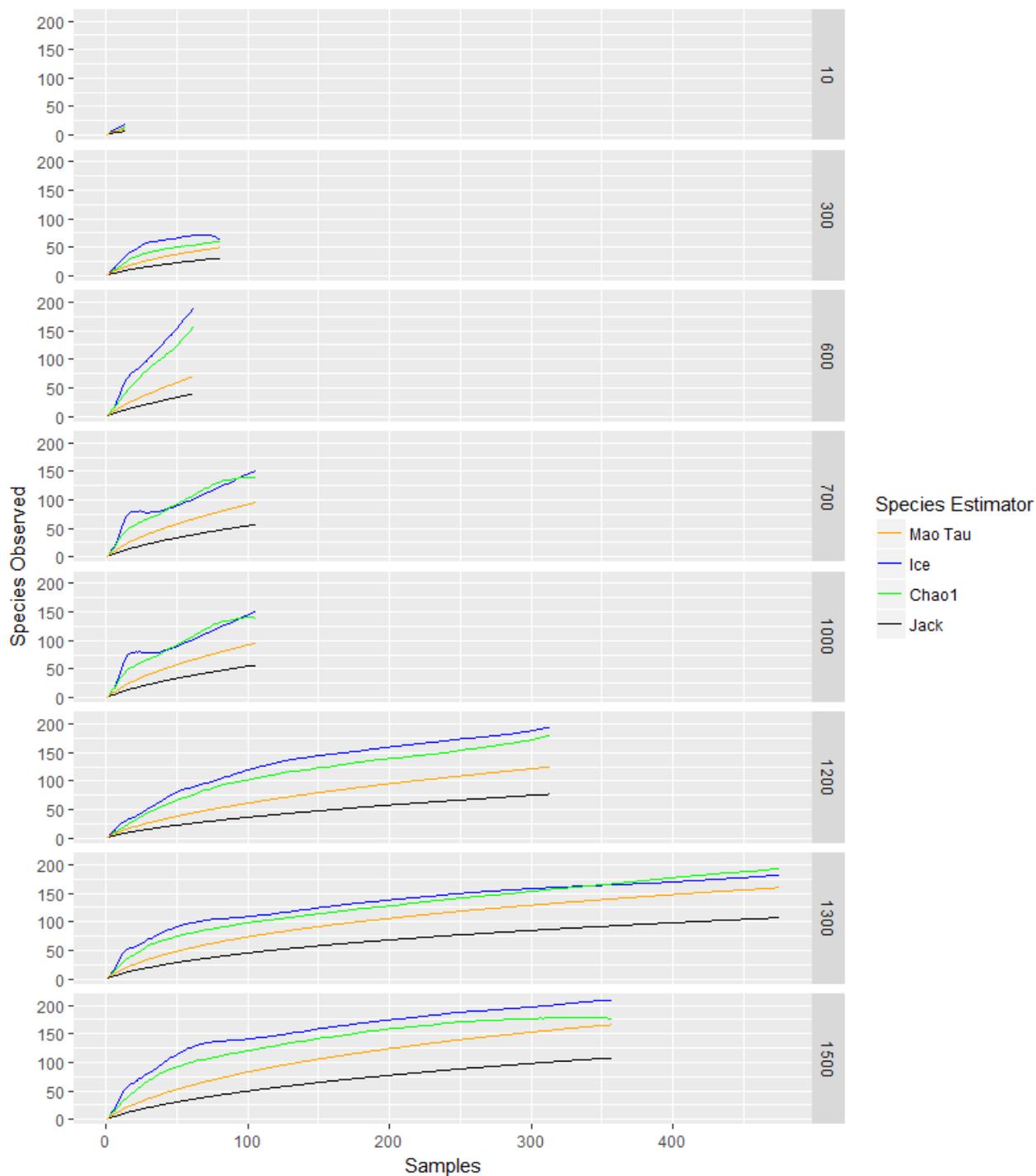


Figure S2. Observed species estimators (using BINs) run 1000 times to calculate observed species (Mao Tau (Colwell et al. 2004), ICE mean (Colwell et al. 2012), CHAO 1 Mean (Chao et al. 2005), and Jack 1 Mean (Colwell et al. 2012) at each elevation sites.

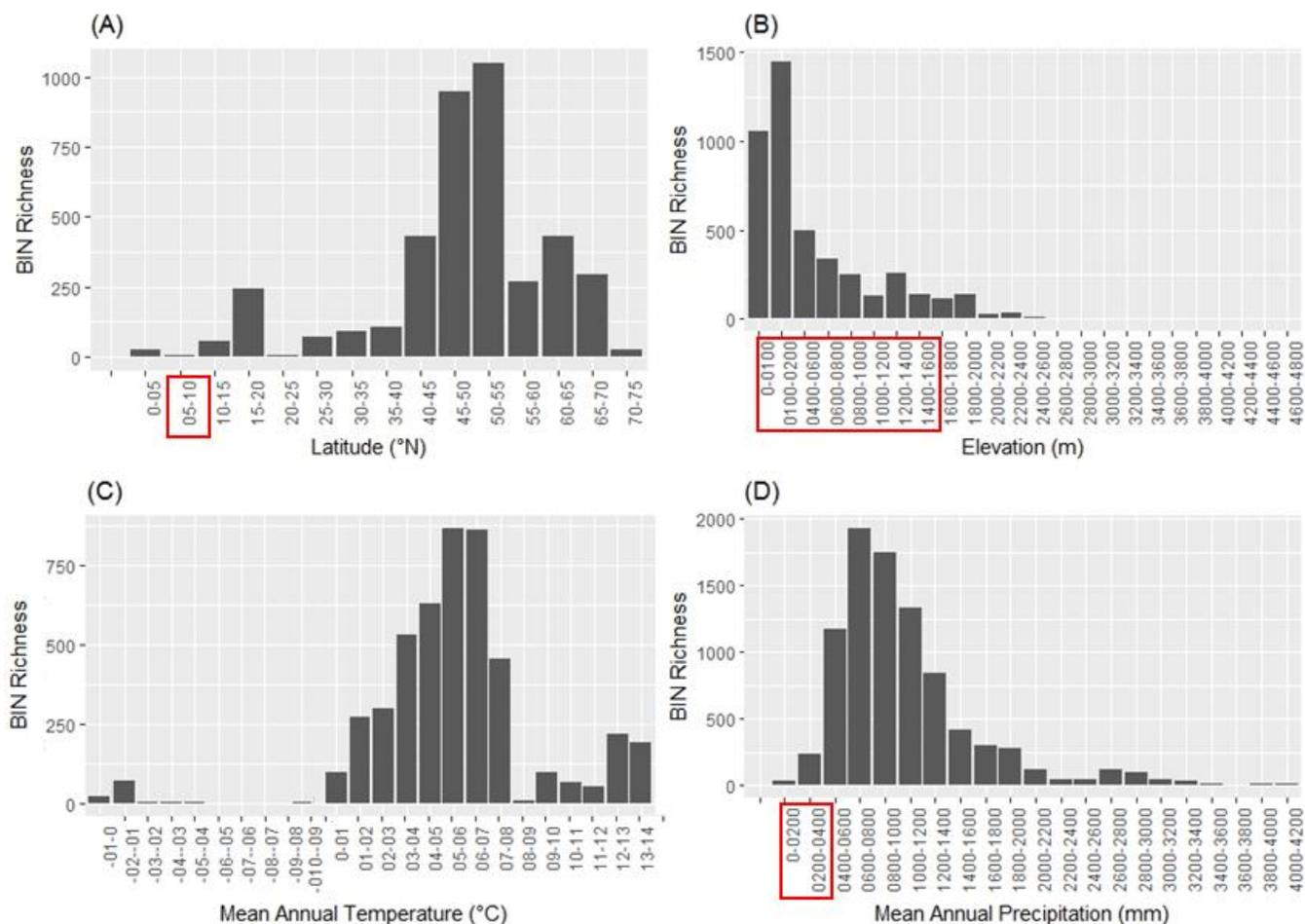


Figure S3. BIN richness across latitudinal categories of 5° of all publically accessible staphylinid records on BOLD (Accessed 18-06-01, total records = 56,501, total BINS = 4051; http://v3.boldsystems.org/index.php/API_Public/combined?taxon=Staphylinidae&format=xml), and BIN richness with the abiotic factors that co-vary with latitude: (B) Elevation, (C) Mean Annual Temperature, and (D) Mean Annual Precipitation. Red boxes indicate where the ACG study system is included. No box is present for temperature because mean annual temperature in Costa Rica is hotter than is present in this graph. Climate data downloaded from WorldClim (<http://www.worldclim.org>; (Hijmans et al., 2005)).