# Determinants of Species Richness and Trait Diversity in Galapagos' Native Biota

A Thesis
Presented in Partial Fulfillment of the Requirements for the
Degree of Master of Science
with a
Major in Biology
in the
College of Graduate Studies
University of Idaho
by

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August 2017

**Authorization to Submit Thesis**

This thesis of Yannik E. Roell, submitted for the degree of Master of Science with a Major in Biology and titled "Determinants of Species Richness and Trait Diversity in Galapagos' Native Biota," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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## Abstract

The evolutionary processes involved in species and trait diversification are key to the formation of island biological diversity. The goal of my thesis is to understand how variation in habitat promotes species richness and trait diversity in the biota of the Galapagos archipelago. My first objective is to understand how the dynamics of island formation influences the number of species found on islands. Results of this work suggest that adding landscape complexity improves models of island species richness. Interestingly, landscape complexity significantly contributes to models of species richness only for a subset of taxonomic groups tested. My second objective is to quantify the association between habitat features and variation in morphology and physiology of endemic land snail species. Results indicate that using cloud cover and shell shape as proxies for climate and morphology, respectively, climate has a positive effect on physiology whereas morphology has a negative effect on physiology.

## Acknowledgements

I thank my advisor, Dr. Christine, E. Parent, for all the time she gave to help with my thesis. Her expertise, insights, encouragement, and experiences were crucial to the finishing of my degree. I thank my committee members: Dr. Luke Harmon and Dr. Ryan Long for the different insights that they brought and always having an open door to ask questions. In addition, I would like to thank all faculty, staff, and fellow students that were always there to talk through difficult parts of the thesis, especially the Statistical Consulting Center for helping with the statistical portions of my work.

**Dedication**

To my family

For the constant love and support

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# Chapter 1: The habitat determinants of island biodiversity

## *Research Goal*

The goal of the research presented in my thesis is to understand how variation in habitat can promote species richness and trait diversity in the Galapagos archipelago. The first objective of this project is to characterize how island ontogeny shapes the number of species found on islands. The second objective is to quantify the association between habitat features and variation in morphology and physiology of species.

## *Galapagos Islands*

This research is being conducted in the Galapagos Islands which are located in the Pacific Ocean with the core islands between 89.2°W and 91.7°W and 0.65°N and 1.42°S. These islands are approximately 1,000 kilometers west of the coast of Ecuador and are a province of that country. Over 8,000 $km^2$ of land is divided into 13 major islands that are larger than 10 $km^2$, six smaller islands, and over 40 islets with names (Snell et al. 1996), all of which are ranging in maximum elevation from 30 to 1,705 meters (Figure 1.1). Of these islands, only four have permanent human residence and many of the other islands are visited daily by tours. Isabela, the largest island at 4,588 $km^2$, is divided into six volcanos that are connected mainly by barren lava fields.

Even though the Galapagos Islands straddle the equator, the islands are much drier than other tropic locations and the climate is mainly influenced by the ocean and prevailing wind currents causing two distinct seasons (Grant 1999). The warm season typically occurs between January and May and although the sky is usually clear, the occasional heavy showers will occur. The cool season typically occurs between June and December and usually has overcast skies but the low lands experience little precipitation.

With the isolation from the mainland and multiple islands in the archipelago for replicated studies, island systems create simpler biological studies than most continental systems. Isolation and multiple islands is important for the present work, especially for the first objective, because the model being tested is based on the theory of island biogeography (MacArthur and Wilson 1963, 1967), which has isolation and area of islands as main

determinants of species richness. Furthermore, having a simpler study system allows for species to be accounted for more easily since there is less area to monitor than continental studies. The Galapagos Islands are no exception and with the islands being a conceptual landmark for evolutionary studies (Darwin 1859), many researchers have made these islands their study system. The endemic land snails of the Galapagos in the genus *Naesiotus* have been thoroughly studied by the Parent Lab at the University of Idaho making these snails an ideal system to fulfill my second objective. In particular, the shell morphology for these snails has been well documented in previous work (Parent and Crespi 2009). By collecting physiological data for snails and environmental measurements of the habitats where they are found, I am able to characterize the link between environment, morphology, and physiology in this system.

*Main Findings and Importance*

My work on the first objective concluded that island ontogeny is important to considered when modeling island species richness. In previous models that use island ontogeny, such as the general dynamic model of oceanic island biogeography (GDM, Whittaker et al. 2008), age and area of the island are used as independent variables for predicting species richness across an archipelago. Certain aspects of an island's ontogeny, in particular topographic complexity, are assumed to follow a hump shaped curve. I tested eight common topographic complexity indices and found that none of the indices tested followed a hump shaped curve. Adding a complexity measure of the landscape to the GDM improved the model but only for a subset of taxonomic groups tested. These results suggest that while topographic complexity does not follow a hump shaped curve as predicted, it is an important determinant of species richness on islands, at least for some taxonomic groups.

My work on the second objective concluded that the shell morphology and the habitat where *Naesiotus* were found have significant effects on the metabolic rate of the snails. This work is explicitly linking the effect that morphology and landscape and climate (both aspects of the environment) have on physiology. Physiology for this work was determined from the metabolic rate of the snails, which was measured from the rate of oxygen consumption, rate of carbon dioxide production, and water vapor pressure. In the model proposed, cloud cover and shell shape are used as proxies for climate and morphology, respectively. Climate was found

to have a significant positive effect on physiology (so that snails found in areas with greater annual cloud cover had higher metabolic rate) and morphology was found to have a significant negative effect on physiology (so that snails with rounder shells were found to have a higher metabolic rate).

This research is important because species and trait diversification are major aspects in the formation of island biological diversity. Island biodiversity is shaped by many processes and understanding how these processes lead to species richness and trait diversity is important to understand the origins of diversity. By examining the abiotic differences in many habitats, the relationships between abiotic factors in a habitat and the diversity present can be determined. Future work could include measuring the effect of additional abiotic factors, either by examining more topographic complexity indices for the first objective or more comprehensive variables for climate and landscape for the second objective. The importance of these abiotic variables can be quantified for an array of taxonomic groups or traits present in a single or across multiple island lineages.

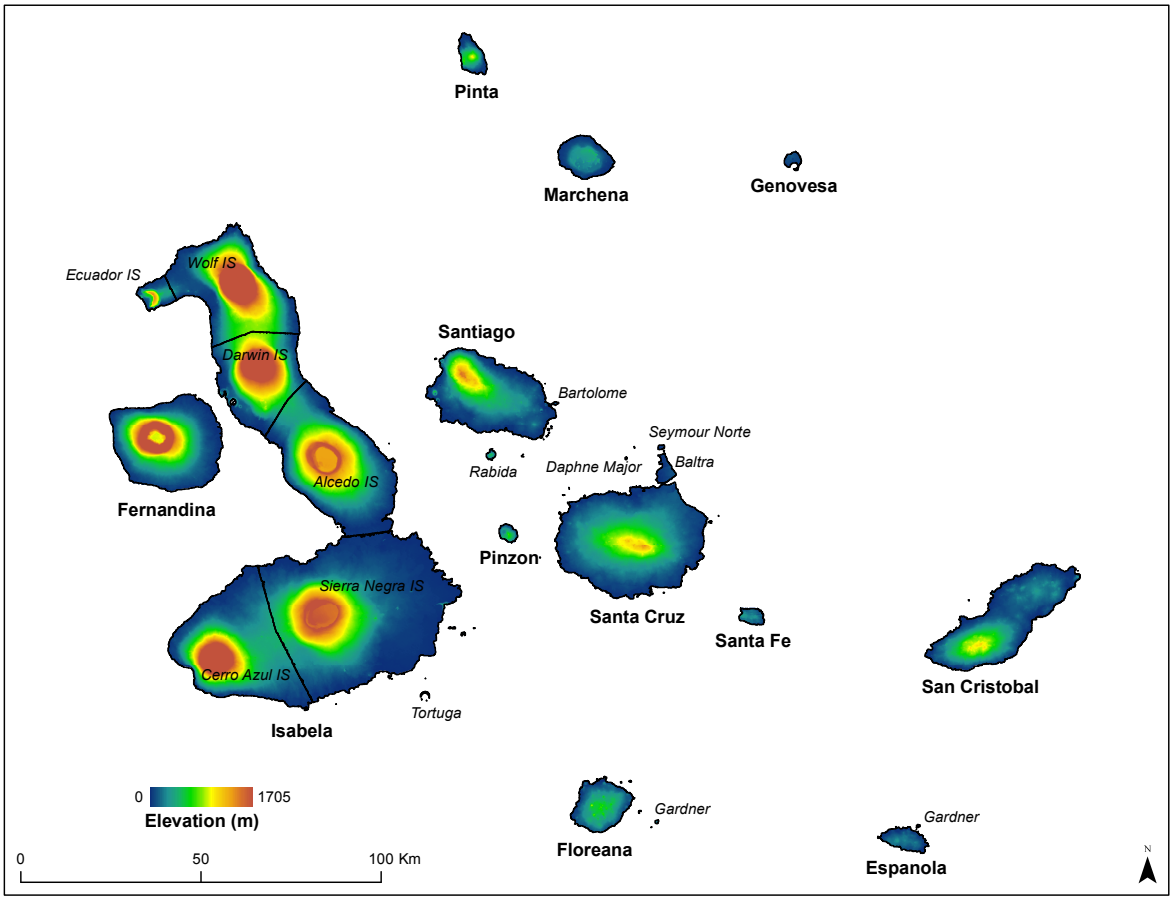


Figure 1.1: Map of Galapagos Islands. Two of the islands, Wolf and Darwin (approximately 150 km northwest of the rest of the islands), are outside the extent of the data collected for determining the landscape variation in chapter 2 and are thus not included on the map. The suffix IS is used to indicate that a given volcano is part of Isabela Island.

**Chapter 2: An empirical test of the role of topographic complexity in the general dynamic model of oceanic island biogeography**

*Yannik Roell and Christine E. Parent*

**Keywords**
topographic complexity, general dynamic model, island biogeography, species richness, Galapagos, volcanic islands

**Abstract:**

The general dynamic model (GDM) of oceanic island biogeography, an extension of the theory of island biogeography (MacArthur and Wilson 1963, 1967), proposes that species richness on islands in a volcanic archipelago is driven by the islands' age and area (Whittaker et al. 2008). Under the GDM, change in topographic complexity of islands over time is assumed to follow a hump shaped curve. However, under the GDM topographic complexity has a verbal description of complexity changing over time but does not have a clear definition that can be quantified. We use species richness data for several taxonomic groups from the Galapagos Archipelago to test whether island topographic complexity, as measured by eight different indices, does predict species richness, as stipulated by the GDM. For each index, we ask whether it significantly contributes to the observed variation in species richness across the islands, and whether its effect over time follows a hump shaped curve as predicted by the GDM. We find no index that consistently contributes to the amount of variation in species richness explained by the GDM across all taxonomic groups considered. However, for four of the 11 taxonomic groups considered, we found that the GDM was improved with the addition of one of the indices of topographic complexity tested. Notably, the variation in species richness across islands for seven of the nine animal taxonomic groups was best explained by a model that solely used habitat diversity (measured as native and endemic plant richness). We also note that species from different taxonomic groups are likely to interact with the landscape at different scales, and thus further work is needed to understand the potential effect of spatial and temporal scales on the effect of topographic complexity in driving species richness.

**Introduction:**

Since the development of the theory of island biogeography by MacArthur and Wilson (1963, 1967), several models linking island ontogeny and biodiversity have been proposed (Paulay 1994; Heaney 2000; Stuessy 2007; Whittaker et al. 2008). In these models, each island in a given archipelago represents a snapshot in time of the island's ontogeny. Since habitat is likely to change over time (e.g., due to changes in abiotic and biotic factors), species present on the islands are predicted to change over time as well. However, modeling how the change of an island's landscape might affect its habitat (and therefore its species diversity) remains a challenge.

The general dynamic model (GDM) of oceanic island biogeography has extended the theory of island biogeography (MacArthur and Wilson 1963, 1967) by taking into account the predictable dynamic changes occurring on volcanic islands to explain species richness (Whittaker et al. 2008). In brief, the GDM proposes that species richness on a given island has an environmentally determined carrying capacity associated with island age resulting from changes over time in the island's area, elevation range, topographic complexity, and habitat diversity. Richness of native and endemic species is predicted to follow a hump shaped curve over time with the greatest number of species found at intermediate island ages when the island reaches its presumed maximum carrying capacity. This pattern is expected because an island's species carrying capacity should peak shortly after the maximum area and elevation are reached, and then slowly decline as erosion reduces both area and elevation (Whittaker et al. 2008).

The GDM relies on the fact that the geological formation of oceanic volcanic islands is remarkably predictable, for the most part. In few words, an island first emerges from the water and gains in size and height quickly reaching its maximum area and elevation at the peak of its volcanic activity (Jackson 2013), early in an island's total lifespan. Subsequently, through a much slower process (Valente et al. 2014), the island erodes and sinks until the landmass is eventually submerged (Jackson 2013). During the erosion process, the landscape shifts and changes and some areas might erode faster than others. This results in uneven surfaces such as hills, valleys, and crevices, which in turn will increase the landscape roughness (i.e., topographic complexity).

The GDM has stimulated new research directions in island biogeography, has withstood rigorous testing of some of its predictions, and has received mixed support for others (Borregaard et al. 2017). One research avenue that has proven to be fruitful is incorporating molecular phylogenies to study lineage radiation across islands. The GDM predicts species on younger islands should diversify quicker than older islands (Whittaker et al. 2008) and this has been supported in two genera of spiders on the Canary Islands (Dimitrov et al. 2008 and Cardoso et al. 2010) and Hawaiian violets (Havran et al. 2009). Other studies have considerably tested the ten predictions derived from the GDM (e.g., Bunnefeld and Phillimore 2012; Cameron et al. 2013; Otto et al. 2016). This includes, for example, testing macroecological properties, such as species abundance distributions and range size of species, using the GDM predictions (Rigal et al. 2013) and determining how the GDM can be applied to trait space instead of just species (Borregaard et al. 2017). However, one assumption that has not been fully explored or tested in-depth is the degree to which topographic complexity follows a hump shaped curve when complexity is quantified. The GDM and some of the subsequent research it has stimulated rely on a verbal description of how topographic complexity is thought to change over time; however, this process remains to be fully characterized.

Topographic complexity has been linked to species richness in many ecosystems (e.g., plants in California [Richerson and Lum 1980], mammals in Australia [Williams et al. 2002], and birds in Western Hemisphere [Ruggiero and Hawkins 2008]). Species differ in the way they interact with the landscape (Stein et al. 2014), and accordingly a range of indices have been used, due to these differences, to measure complexity (Yu et al. 2015). The four most common measurements that are used to evaluate topography include elevation (height of surface above sea level), slope (rate of elevational change over the horizontal surface), curvature (rate of slope change over the surface), and aspect (azimuth direction of slope). These topographical measures might affect organisms, for example, by shaping the water and energy budgets at a given location (Yu et al. 2015). More specifically, elevation has been used as a proxy for many environmental factors, including air temperature, atmospheric pressure, and wind speed (Yu et al. 2015). In contrast, slope and curvature affect how fast water runs and soil erodes, and where water and soil accumulate (Gosz and Sharpe 1989). Finally, aspect influences the amount of solar light that a location will receive (Yu et al. 2015). Although

studies have evaluated the effects of topography in many different systems, there is no clear agreement on a common measure to compare complexities across different landscapes, and how these measures of topographic complexity might change over time.

The GDM assumes that topographic complexity is greatest at intermediate island ages. At that stage, the landscape is being heavily eroded and changing quickly. However, measuring landscape complexity is challenging. Many topographic indices have been proposed to capture complexity, but none of these indices can capture all components of an intricate landscape. For example, a landscape can have a high level of curvature (high complexity) but low level of slope (low complexity). Thus, with using only one index, some component of complexity will be missed. Importantly, species richness for different taxonomic groups will likely be affected differently by different aspects of topographic complexity and it is therefore unlikely that a single index of topographic complexity will capture how landscape dynamics might affect diversity across islands.

To better characterize how island ontogeny and its associated changes in topographic complexity influences the number of species found on islands, we use the Galapagos Archipelago as the study system. Galapagos has a relatively well understood geological history (Geist 1996), allowing for each island to have a fairly accurate island age. With this island group being such a crucial part of our understanding of evolutionary biology (Grant and Grant 2008) and having fewer species diversifications than other Pacific island groups (Parent 2008), the distribution of species across the archipelago is well documented. The publicly available species distribution data for each island in the Galapagos from the Charles Darwin Foundation allows for a convenient way to determine the effect of a topographic complexity index on the GDM with a large range of taxonomic groups.

In this study, we first test whether a range of commonly used indices of topographic complexity follow a hump shaped curve as assumed by the GDM. We then incorporate measurements of topographic complexity in the GDM in the form of eight possible indices to predict how species richness changes in 11 distinct taxonomic groups (terrestrial vertebrates, invertebrates, and plants) as Galapagos oceanic islands form and disappear. By understanding the relationship between complex landscapes and species richness, models linking island ontogeny and biodiversity can explain more of the variability in species distribution across an archipelago.

**Materials and Methods:**

*Island Species Richness Data*

Galapagos species distribution data were obtained from the Charles Darwin Foundation Datazone (CDFD, Bungartz et al. 2009) (Table 2.1), which included terrestrial species that are native or endemic to Galapagos. Because our analyses focus on the influence of topographic complexities of the terrestrial landscape on species richness, we excluded animals that are partly relying on marine habitats (marine mammals, marine iguanas, and sea birds). We also included vascular plants and bryophytes, the only plants that were included from the CDFD. For our analyses, we used the native and endemic species for the following taxonomic groups: plants, vertebrates, mammals, reptiles, land birds, and invertebrates. We also performed the same analyses using the number of single island endemic (SIE) species on each given island (i.e., species with distributions restricted to a single island) for plants, vertebrates, and invertebrates. Finally, we ran additional analyses using a dataset of endemic terrestrial snails all pertaining to a single adaptive radiation for which more complete and higher spatial resolution range maps are available (Table 2.2). This dataset includes 25 islands (compared to the 14 islands for the other CDFD datasets). One important difference between all the CDFD datasets and the snail dataset is that for the latter, Isabela Island is separated into six separate islands (one per major volcano) whereas the former datasets report species presence on that island as a whole. For most terrestrial and low dispersing organisms, the volcanos of Isabela Island can be viewed as separate islands as they are isolated from one another by kilometers of barren lava flows. However, only for the land snail dataset do we have information about distribution at the volcano level available allowing for this partition.

*Outline of Suitable Terrestrial Habitat*

A common approach in evaluating the effect topographic complexity has on species richness and distribution is to measure the entire landscape as a potential habitat (Everson and Boucher 1998; Chapman and Underwood 1994), as being done for the CDFD species data. However, using the entire landscape can be misleading as many of its regions might represent unsuitable habitat to organisms. Human settlements and lava fields are two examples of an island landscape that are uninhabitable for most native and endemic species. The normalized difference vegetation index (NDVI), a measure of aboveground net primary productivity from

satellite imaging, is one way for these areas of unsuitable land to be eliminated from the landscape, thereby restricting the characterization of topographic complexity to the suitable landscape for native and endemic species (Pettorelli et al. 2005). NDVI can be calculated anywhere on the planet and is computed as (NIR-Red)/(NIR+Red) with NIR and Red being the amount of near-infrared and red light being reflected from the surface (Rouse et al. 1974). Since green leaves strongly absorb in the blue and red region of the light spectrum, a positive NDVI value is indicative of vegetation. Negative and near zero NDVI values indicate areas on the landscape that have low to no healthy green vegetation such as cement or water. These values have become common ways for ecological studies to monitor biodiversity (Durant et al. 2005; Pettorelli et al. 2011).

A map of NDVI for the Galapagos was created in Esri's ArcMap 10.3.1 from data collected in early May 2014 by using satellite (Landsat 7) Level 1 Product downloaded from USGS EarthExplorer (USGS 2014). To determine where the landscape was unsuitable, all locations that have been sampled for snails using GPS points from 2001 to 2016 by the Parent Lab at the University of Idaho were overlaid on the NDVI raster (Figure 2.1). An NDVI value of -0.35 was used to include all snail GPS points but exclude areas where snails are not inhabiting. Only NDVI is being incorporated with the snail dataset because we know for sure where the limit of the snail's range is on the islands. Using this value distinguished between areas that are livable and non-livable for these snail species. By doing this, much of the younger island area with lava flows were excluded from the landscape analysis. This allows for a better analysis on how topographic complexity affects the overall species richness of terrestrial snail distribution since many parts of the islands are not suitable for certain species. For area and island topographic complexity described below, the islands were also clipped to the extent of the NDVI layer before running the zonal statistic tool. This allowed us to obtain the area and island topographic complexity for the full island and the NDVI island extent separately.

*Island Isolation, Area, and Age*

For each island and Isabela volcano, we computed measures of island isolation, area, and age. The volcanos on Isabela were separated into individual islands by using ArcMap. The area with the lowest elevation of the lava fields between two volcanos was used as the

dividing line to separate the volcanos. Isolation of each island was calculated using the generate near table tool in ArcMap, which obtains a mean distance between the focal and all other islands. The island area was calculated by using the zonal statistics tool in ArcMap. The isolation and area for the islands of Darwin and Wolf were excluded because these islands were outside of the geographic extent of the shapefile available in ArcMap. Island age was acquired from Geist et al. 2014.

*Island Topographic Complexity*

A key component of our study is the quantification of island topographic complexity. We calculated topographic complexity based on the highest resolution (30-meter resolution) digital elevation model (DEM) available for Galapagos. We excluded the islands of Darwin and Wolf when computing the topographic complexity due to these islands being outside the geographical extent of the available DEM. The DEM was downloaded from USGS Global Data Explorer using the NASA Shuttle Radar Topography Mission (SRTM) 1 arc-sec data (NASA 2013). We created three rasters from the DEM (Figure 2.2): slope (using the Spatial Analyst Toolbox from ArcMap), total curvature, and rugosity (the last two using the DEM Surface Tools extension from Jennessent (Jenness 2013)). The zonal statistic tool in ArcMap was used to compute indices at the island level. The topographic indices used were range of elevation, standard deviation of elevation, range of slope, standard deviation of slope, total curvature, standard deviation of curvature, rugosity, and compound terrain complexity index (CTCI, Lu et al. 2007). CTCI uses range of elevation, standard deviation of elevation, total curvature, and rugosity to depict the landscape from common indices used (Yu et al. 2015). Standard deviation of curvature was calculated from a raster of general curvature, which, unlike total curvature, does not restrict values and allows for positive and negative values. All computed indices are reported in Tables 2.3-2.5.

*Statistical Analyses*

Generalized linear models were run on each taxonomic dataset from the CDFD and the additional snail dataset with full landscape and suitable landscape as determined via NDVI for a total of 11 taxonomic datasets. The datasets were: native + endemic and SIE plants, native + endemic and SIE vertebrates, native + endemic mammals, native + endemic reptiles,

native + endemic birds, native + endemic and SIE invertebrates, and full landscape snails and NDVI snails. Each taxonomic dataset was used to test a series of models that was some variation of the GDM: log Area + Time + Time$^2$ (ATT$^2$). The plant datasets had eight models tested: five simpler models (Time, Time$^2$, log Area, isolation, and Time + Time$^2$), the GDM (ATT$^2$), and two extensions to the GDM (ATT$^2$ + isolation and ATT$^2$ + isolation + topographic complexity). For the animal datasets, the number of native and endemic plant species found on each island was included as a proxy for habitat diversity (Parent et al. 2008). To obtain habitat diversity for the snail dataset, the plant species richness for each island was acquired from C.E. Parent (unpublished). The animal datasets had 10 models tested: six simpler models (Time, Time$^2$, log Area, isolation, habitat diversity, and Time + Time$^2$), the GDM (ATT$^2$), and three extensions to the GDM (ATT$^2$ + isolation, ATT$^2$ + isolation + habitat diversity, and ATT$^2$ + isolation + habitat diversity + topographic complexity). The eight topographic complexity indices were added one at a time to identify the index that best describes the landscape for each dataset. Thus, with the topographic complexity indices being tested individually, 15 models were tested for the plant datasets and 17 models tested for the animal datasets. Table 2.6 summarizes the results with $R^2$, adjusted $R^2$, p values, and Akaike's information criterion (AIC) values reported for each model that was significant (p value < 0.05). A likelihood ratio test (LRT) was run on the GDM and all extensions to determine if any GDM extension is significantly better at explaining variation in species richness. Since the LRT requires nested models, the GDM was not compared to the simpler models due to the GDM not incorporating all of the variables in the simpler models (isolation and habitat diversity). The LRT p values are reported in Table 2.6 for models that were extensions to the GDM. All statistical analyzes were performed in R.

**Results:**

When considering all of the models run, different models were the best model (i.e., models with the lowest AIC) at explaining species richness for different taxonomic datasets. There was no single model that fits the data best for all datasets. Seven of the datasets (native + endemic plants, native + endemic vertebrates, native + endemic reptiles, native + endemic birds, native + endemic invertebrates, full landscape snails, and NDVI landscape snails) had the original GDM (ATT$^2$) as being significant at explaining the species richness across the

Galapagos archipelago. The same seven datasets had at least one of the GDM extensions as being significant at explaining species richness. An extension to the GDM including a topographic complexity index was significant for six of the seven datasets (native + endemic reptiles was the one taxonomic dataset that did not have an extension including a complexity index). The only topographic complexity index that was significant for all of the six datasets that included a model with a complexity index, was range of slope. Of the six datasets with a significant GDM extension including a complexity index, four datasets (native + endemic birds, native + endemic invertebrates, full landscape snails, and NDVI landscape snails) indicated that the GDM extensions were significantly different from the GDM using the LRT. For animal taxonomic datasets, using the number of native and endemic plant species as a measure of habitat diversity to explain species richness variation was always significant. For seven of the nine animal taxonomic datasets considered, the best model explaining species richness across the islands was the model including habitat diversity only. The complete list of results for significant models is reported in Table 1. Below we detail the results of our model testing, one taxonomic group at a time.

*Plants*

The variation in the number of native + endemic plant species across islands was best explained by $ATT^2$ + isolation (the simpler $ATT^2$ model had a higher but not significantly different AIC score). All eight GDM extensions including the topographic complexity indices (range and standard deviation of elevation, range and standard deviation of slope, total curvature, standard deviation of curvature, rugosity, and CTCI) were significant and had a $\Delta$AIC less than 2. However, the LRT indicated that none of the GDM extensions were significantly different then the simpler GDM. None of the models tested significantly explained the variation SIE plant species number across the archipelago.

*Vertebrates*

The variation in both native + endemic and SIE vertebrate species richness were best explained by the model including habitat diversity only. Six additional models (out of 17 tested) also significantly explained the variation in the number of native + endemic vertebrate species across the archipelago, but to a lesser extent than the habitat diversity model.

Extensions of the GDM ($ATT^2$ + any other variable) were not significantly different than the simpler $ATT^2$ GDM.

For the native + endemic mammals, the model including habitat diversity as the sole explanatory variable was the only significant model. The number of native + endemic reptile species across the islands was best explained by a model that included habitat diversity only. Of the other significant models for native + endemic reptiles, $ATT^2$ and $ATT^2$ + isolation were both significant but not statistically different from each other. Variation in native + endemic land bird species across the archipelago was best explained by $ATT^2$ + isolation + habitat diversity. The GDM extensions were all significant and had a $\Delta$AIC less than 2. The LRT indicated that all of the models using the GDM variables plus additional variables (isolation, habitat diversity, and all eight topographic complexity indices) were significantly better than the simpler $ATT^2$ for the variation in native + endemic land bird species.

*Invertebrates*

The variation in both the number of native + endemic and SIE invertebrate species was best explained by the model using habitat diversity only. Habitat diversity was the only significant model for SIE invertebrates but for native + endemic invertebrates, 12 of the 17 other models considered were also significant. All of the extended GDM models that included a topographic complexity to explain the variation in native + endemic invertebrate species were significant except the model using standard deviation of elevation as the topographic index. Using the LRT, all models explaining variation in native + endemic invertebrate species across the islands representing extensions of the GDM ($ATT^2$ + other variable(s)) were significantly better than the simpler GDM except for the $ATT^2$ + isolation model.

*Snails*

The snail datasets, which consisted of 25 islands and separated Isabela into six islands, one for each volcano, instead of the 14 islands for the rest of the datasets, was divided into two datasets. The first dataset considers the complete landscape to compute the biogeographic variables (referred to as the full landscape snail dataset) whereas the second is reduced to the suitable snail habitat using the NDVI information (referred to as the NDVI landscape snail dataset). Using the full landscape snail dataset, the variation in snails across the islands was

best explained by the model only using habitat diversity. The GDM and all of the models using the GDM + additional variables were significant but none of these models had a ΔAIC less than 2. The LRT indicated that all models using the GDM variables + other variables were significantly different from the GDM except the model using GDM + isolation. By taking the NDVI into consideration, the model using the GDM variables with rugosity as the topographic index best explained the variation in the number of snail species across the islands. The GDM and all of the GDM extensions had a ΔAIC less than 2 except for the model using range of slope as the topographic index. All of the GDM extension models were significantly different than the GDM according to the LRT except for the model using the GDM + isolation, the model including standard deviation of elevation as the topographic index, and the model including range of slope as the topographic index.

**Discussion:**

*Habitat Diversity and Isolation*

For all non-plant taxonomic groups, the only model that was significant for all groups was the model that included habitat diversity as the sole explanatory. Before the GDM was formulated, Parent & Crespi (2006) demonstrated that habitat diversity explains a larger portion of variation in island species richness than island area. More isolated islands are likely to have lower species richness since the likelihood of successful colonization for most species decreases with between island distance (Ricklefs and Bermingham 2004). With isolation having a crucial impact on species richness by effecting the colonization rate of new species (MacArthur and Wilson 1963, 1967), we decided to incorporate isolation along with habitat diversity as additional variables to test with the GDM.

*Topographic complexity*

In the GDM, topographic complexity is not explicitly considered but is rather assumed to follow a hump shaped curve with age of the island. None of the different measures of topographic complexity of Galapagos Islands followed the expected hump shaped curve. Conceptually, the idea that topographic complexity should follow a hump shaped curve is appealing. Since a common method of measuring complexity is using range of elevation, a volcanic island would be highly complex after the volcano has reached a maximum elevation.

Allowing for erosion to occur after the maximum elevation has been reached, the topographic complexity would be the highest during this intermediate age until erosion has caused the peak elevation to decrease. Although one index might capture part of the complexity, using one index to measure complexity does not capture the entire landscapes complexity so generalization is occurring on the landscape. Thus, the GDM assumes that topographic complexity follows a hump shaped curve but this assumption does not hold true for the Galapagos Islands when using one index to explain complexity.

After running the models, the variation in the number of species for seven taxonomic groups was significantly explained by the GDM. From these seven groups, models that included the GDM variables with additional variables was significantly different from the GDM for four of the taxonomic groups. By comparing the GDM to the models with the GDM plus other variables, models that included a measure of topographic complexity always had a higher adjusted $R^2$ value than the GDM alone. Although the use of an index to measure topographic complexity in the GDM was not always significantly different from the GDM alone, when the models were different according to the LRT, the indices improved the GDM. This indicates that the indices can improve the GDM but the use of an index is taxonomic group specific.

*Taxonomic Differences*

Since each taxonomic group interacts with the landscape at a specific scale, studies have shown that the scale at which the topographic complexity is used to predict species richness is critical (Yu et al. 2015). For species that have high dispersal ability, such as birds or wind dispersed plants, complexity indices at a fine scale are not needed, due to the movement ability of the species. For birds and wind dispersed plants, the change in a landscape that occurs every meter might not be as important as the change in a landscape that occurs every 100 meters. For species that have low dispersal ability, such as snails or many plants, complexity indices at a fine scale would be needed to understand how these species interact with the landscape. For species that might only move a few meters in a life span, the variation in the landscape at the sub-meter level is crucial but the variation across an entire island is not relevant.

Due to the scale limitation in the DEM data, minute differences in the landscape are not being detected. Although Wright et al. (2006) found that data re-sampled to a coarser resolution (e.g. 10-meter cells to 30-meter cells) did not have a large effect on the overall topology, the minor differences in the land missed with lower resolution data causes issues when modeling many taxonomic groups. Since more DEM errors occur in more complex landscapes (Gao 1997) and the topographic indices are created from the DEM, there will be more uncertainty in species that might only have a range of 30 square meters (size of 1 cell). Incorporating one scale for all species limits the use of topographic complexities in modeling species richness.

*Normalized Difference Vegetation Index Effect*

Using NDVI as a way to only incorporate areas of interest for the snails, the models had higher adjusted $R^2$ values than the snail models that used the entire landscape, except for the habitat diversity model. The range of values that were better were between 0.085 and 0.292 with an average of 0.138. The use of NDVI has been shown to increase analysis in ecological studies (Pettorelli et al. 2011) and has improved modeling species distribution and abundance (Bro-Jorgensen et al. 2009; Evans et al. 2008). NDVI was not incorporated with any of the other taxonomic groups besides snails because specific collection sites were not included in the data from the CDFD. With more information of specific species distribution, NDVI could be incorporated for all species.

When NDVI is implemented to eliminate certain areas, the time that the satellite image was collected should be considered. For the Galapagos, there are two seasons: wet and dry, which are roughly between December to May and June to November, respectively (Grant and Boag 1980). The value of -0.35 that was used as the threshold to incorporate all of the snail GPS points only works for the specific NDVI data used for this study. If the NDVI was collected in any other month instead, the value needed to incorporate all of the GPS points would be a different value.

**Conclusions:**

The GDM assumption about topographic complexity being hump shaped did not hold true for the Galapagos using the taxonomic groups in this paper. However, the addition of

topographic complexity indices did enhance the model for some of the taxonomic groups. Habitat diversity was found to be a crucial aspect in predicting species richness, just as Parent and Crespi (2006) stated. Understanding the interaction between species and the landscape needs to be assessed for topographic complexity indices to be incorporated fully into the GDM. Multiple scales of the landscape should be evaluated for each taxonomic group in future work to see how scale effects the outcome of using these indices in the GDM.

Table 2.1: Species distribution for data from Charles Darwin Foundation Datazone. The taxonomic groups are: native plants (NP), native vertebrates (NV), native birds (NB), native mammals (NM), native reptiles (NR), native invertebrates (NI), single island endemic plants (SIEP), single island endemic vertebrates (SIEV), and single island endemic invertebrates (SIEI).

| Island | NP | NV | NB | NM | NR | NI | SIEP | SIEV | SIEI |
|---|---|---|---|---|---|---|---|---|---|
| **Darwin** | 17 | 3 | 3 | 0 | 0 | 26 | 0 | 0 | 1 |
| **Espanola** | 110 | 11 | 8 | 0 | 3 | 175 | 0 | 0 | 5 |
| **Fernandina** | 186 | 21 | 14 | 2 | 5 | 247 | 1 | 3 | 2 |
| **Floreana** | 263 | 28 | 20 | 1 | 7 | 412 | 7 | 2 | 9 |
| **Genovesa** | 50 | 9 | 8 | 0 | 1 | 117 | 0 | 0 | 1 |
| **Isabela** | 405 | 34 | 21 | 1 | 12 | 616 | 24 | 5 | 44 |
| **Marchena** | 58 | 13 | 11 | 0 | 2 | 182 | 0 | 0 | 1 |
| **Pinta** | 199 | 15 | 13 | 0 | 2 | 238 | 2 | 2 | 0 |
| **Pinzon** | 118 | 14 | 11 | 0 | 3 | 150 | 5 | 1 | 2 |
| **San Cristobal** | 320 | 23 | 15 | 1 | 7 | 428 | 16 | 3 | 16 |
| **Santa Cruz** | 479 | 58 | 26 | 10 | 22 | 1195 | 68 | 16 | 428 |
| **Santa Fe** | 76 | 18 | 11 | 1 | 6 | 158 | 1 | 3 | 1 |
| **Santiago** | 322 | 24 | 16 | 2 | 6 | 404 | 7 | 3 | 4 |
| **Wolf** | 28 | 7 | 6 | 0 | 1 | 51 | 0 | 1 | 1 |

Table 2.2: Species distribution for extended snail dataset with native plants (NP). For the six volcanos that encompass Isabela, IS after the name indicates that it is part of Isabela.

| Island | NP | Snails |
|---|---|---|
| **Alcedo IS** | 254 | 4 |
| **Baltra** | 61 | 1 |
| **Bartolome** | 4 | 1 |
| **Cerro Azul IS** | 172 | 6 |
| **Daphne Major** | 33 | 1 |
| **Darwin IS** | 160 | 2 |
| **Ecuador IS** | 24 | 1 |
| **Espanola** | 105 | 4 |
| **Fernandina** | 189 | 4 |
| **Floreana** | 243 | 14 |
| **Gardner ES** | 56 | 1 |
| **Gardner FL** | 9 | 1 |
| **Genovesa** | 63 | 0 |
| **Marchena** | 57 | 0 |
| **Pinta** | 170 | 1 |
| **Pinzon** | 114 | 5 |
| **Rabida** | 93 | 2 |
| **San Cristobal** | 282 | 13 |
| **Santa Cruz** | 392 | 27 |
| **Santa Fe** | 77 | 1 |
| **Santiago** | 286 | 8 |
| **Seymour Norte** | 52 | 0 |
| **Sierra Negra IS** | 298 | 3 |
| **Tortuga** | 3 | 1 |
| **Wolf IS** | 68 | 4 |

Table 2.3: General dynamic model variables (Age, Area, and Isolation) and topographic complexity indices for the Charles Darwin Foundation Datazone species distribution. The topographic complexity indices are: range of elevation (RE), standard deviation of elevation (SE), range of slope (RS), standard deviation of slope (SS), total curvature (TC), standard deviation of curvature (SC), rugosity (RU), and compound terrain complexity index (CTCI).

| Island | Age (Ma) | Area ($m^2$) | Isolation (m) | RE | SE | RS | SS | TC | SC | RU | CTCI |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Darwin** | 0.4 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| **Espanola** | 3.2 | 60570000 | 144162 | 210 | 43.0 | 55.5 | 4.3 | 0.00186 | 0.62220 | 1.01000 | 0.12252 |
| **Fernandina** | 0.06 | 637440000 | 125312 | 1480 | 352.3 | 80.8 | 6.9 | 0.00112 | 0.51276 | 1.01778 | 0.55685 |
| **Floreana** | 1.9 | 172250000 | 103491 | 568 | 106.3 | 56.8 | 5.1 | 0.00095 | 0.50161 | 1.01195 | 0.20025 |
| **Genovesa** | 0.4 | 13920000 | 140115 | 76 | 16.6 | 40.4 | 3.8 | 0.00109 | 0.51463 | 1.00682 | 0.03906 |
| **Isabela** | 0.6 | 4607130000 | 58287 | 1705 | 339.5 | 83.2 | 5.4 | 0.00097 | 0.47324 | 1.01074 | 0.54368 |
| **Marchena** | 0.4 | 130000000 | 122268 | 335 | 74.6 | 47.3 | 4.6 | 0.00073 | 0.43775 | 1.00835 | 0.11599 |
| **Pinta** | 0.4 | 59140000 | 146342 | 633 | 149.2 | 70.4 | 6.9 | 0.00316 | 0.81577 | 1.02730 | 0.39495 |
| **Pinzon** | 1.5 | 18310000 | 72167 | 455 | 106.3 | 74.7 | 8.7 | 0.00725 | 1.24450 | 1.05722 | 0.62497 |
| **San Cristobal** | 3.2 | 556410000 | 142778 | 718 | 143.0 | 53.2 | 3.6 | 0.00078 | 0.44149 | 1.00715 | 0.22199 |
| **Santa Cruz** | 1.8 | 985170000 | 73208 | 862 | 159.2 | 48.6 | 2.6 | 0.00041 | 0.31978 | 1.00371 | 0.22679 |
| **Santa Fe** | 2.6 | 25000000 | 91066 | 266 | 50.0 | 61.0 | 8.3 | 0.00563 | 1.15450 | 1.03354 | 0.38424 |
| **Santiago** | 0.7 | 577840000 | 79272 | 909 | 185.8 | 71.9 | 4.5 | 0.00083 | 0.45099 | 1.00884 | 0.29297 |
| **Wolf** | 1.7 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |

Table 2.4: General dynamic model variables (Age, Area, and Isolation) and topographic complexity indices for the snail dataset considering the full island. The topographic complexity indices are: range of elevation (RE), standard deviation of elevation (SE), range of slope (RS), standard deviation of slope (SS), total curvature (TC), standard deviation of curvature (SC), rugosity (RU), and compound terrain complexity index (CTCI). For the six volcanos that encompass Isabela, IS after the name indicates that it is part of Isabela.

| Island | Age (Ma) | Area ($m^2$) | Isolation (m) | RE | SE | RS | SS | TC | SC | RU | CTCI |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Alcedo IS** | 0.4 | 888300000 | 91989 | 1173 | 278.3 | 56.2 | 4.2 | 0.00059 | 0.37935 | 1.00807 | 0.34065 |
| **Baltra** | 1.8 | 25420000 | 76848 | 70 | 17.5 | 44.0 | 3.1 | 0.00087 | 0.43164 | 1.00458 | 0.01276 |
| **Bartolome** | 0.01 | 1220000 | 76897 | 100 | 21.5 | 35.6 | 6.1 | 0.00272 | 0.80754 | 1.02710 | 0.05383 |
| **Cerro Azul IS** | 0.3 | 852580000 | 117388 | 1677 | 363.2 | 73.0 | 5.4 | 0.00076 | 0.42727 | 1.01103 | 0.47233 |
| **Daphne Major** | 0.02 | 320000 | 74135 | 98 | 30.7 | 50.5 | 11.9 | 0.02843 | 2.46121 | 1.13881 | 0.30119 |
| **Darwin IS** | 0.6 | 500830000 | 110188 | 1408 | 377.8 | 63.9 | 5.7 | 0.00091 | 0.47245 | 1.01537 | 0.44660 |
| **Ecuador IS** | 0.3 | 62510000 | 138730 | 893 | 214.2 | 83.2 | 13.2 | 0.02343 | 2.21869 | 1.08276 | 0.44620 |
| **Espanola** | 3.2 | 59510000 | 144162 | 210 | 43.0 | 55.5 | 4.3 | 0.00186 | 0.62220 | 1.01000 | 0.05999 |
| **Fernandina** | 0.06 | 637570000 | 125312 | 1480 | 352.3 | 80.8 | 6.9 | 0.00112 | 0.51276 | 1.01778 | 0.44546 |
| **Floreana** | 1.9 | 172330000 | 103491 | 568 | 106.3 | 56.8 | 5.1 | 0.00095 | 0.50161 | 1.01195 | 0.15063 |
| **Gardner ES** | 2.5 | 520000 | 144430 | 53 | 11.2 | 24.1 | 3.6 | 0.00153 | 0.58586 | 1.01199 | 0.01782 |
| **Gardner FL** | 0.9 | 820000 | 108785 | 203 | 61.7 | 66.9 | 16.7 | 0.05700 | 3.22721 | 1.22104 | 0.55677 |
| **Genovesa** | 0.4 | 13270000 | 140115 | 76 | 16.6 | 40.4 | 3.8 | 0.00109 | 0.51463 | 1.00682 | 0.01668 |
| **Marchena** | 0.4 | 130030000 | 122268 | 335 | 74.6 | 47.3 | 4.6 | 0.00073 | 0.43775 | 1.00835 | 0.09117 |
| **Pinta** | 0.4 | 59160000 | 146342 | 633 | 149.2 | 70.4 | 6.9 | 0.00316 | 0.81577 | 1.02730 | 0.21408 |
| **Pinzon** | 1.5 | 18320000 | 72167 | 455 | 106.3 | 74.7 | 8.7 | 0.00725 | 1.24450 | 1.05722 | 0.21365 |
| **Rabida** | 1.4 | 5070000 | 74244 | 352 | 90.5 | 53.9 | 8.2 | 0.00564 | 1.14745 | 1.08119 | 0.20895 |
| **San Cristobal** | 3.2 | 552420000 | 142778 | 718 | 143.0 | 53.2 | 3.6 | 0.00078 | 0.44149 | 1.00715 | 0.18935 |
| **Santa Cruz** | 1.8 | 985530000 | 73208 | 862 | 159.2 | 48.6 | 2.6 | 0.00041 | 0.31978 | 1.00371 | 0.21526 |
| **Santa Fe** | 2.6 | 25030000 | 91066 | 266 | 50.0 | 61.0 | 8.3 | 0.00563 | 1.15450 | 1.03354 | 0.11641 |
| **Santiago** | 0.7 | 578090000 | 79272 | 909 | 185.8 | 71.9 | 4.5 | 0.00083 | 0.45099 | 1.00884 | 0.24632 |
| **Seymour Norte** | 1.8 | 2000000 | 78048 | 37 | 9.6 | 22.3 | 2.9 | 0.00078 | 0.41120 | 1.00463 | 0.00268 |
| **Sierra Negra IS** | 0.5 | 1718540000 | 92658 | 1131 | 268.7 | 66.3 | 3.3 | 0.00045 | 0.33270 | 1.00445 | 0.32369 |
| **Tortuga** | 0.5 | 1410000 | 93447 | 113 | 34.1 | 57.2 | 11.9 | 0.02270 | 2.33099 | 1.15918 | 0.30368 |
| **Wolf IS** | 0.5 | 678100000 | 124477 | 1705 | 417.8 | 74.6 | 7.0 | 0.00102 | 0.48655 | 1.01981 | 0.52122 |

Table 2.5: General dynamic model variables (Age, Area, and Isolation) and topographic complexity indices for the snail dataset using the normalized difference vegetation index. The topographic complexity indices are: range of elevation (RE), standard deviation of elevation (SE), range of slope (RS), standard deviation of slope (SS), total curvature (TC), standard deviation of curvature (SC), rugosity (RU), and compound terrain complexity index (CTCI). For the six volcanos that encompass Isabela, IS after the name indicates that it is part of Isabela.

| Island | Age (Ma) | Area ($m^2$) | Isolation (m) | RE | SE | RS | SS | TC | SC | RU | CTCI |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Alcedo IS** | 0.4 | 638330000 | 91989 | 1173 | 279.2 | 56.2 | 4.5 | 0.00068 | 0.40760 | 1.01009 | 0.35543 |
| **Baltra** | 1.8 | 5210000 | 76848 | 62 | 9.1 | 21.2 | 2.5 | 0.00055 | 0.34493 | 1.00327 | 0.00147 |
| **Cerro Azul IS** | 0.3 | 502690000 | 117388 | 1677 | 376.7 | 73.0 | 5.8 | 0.00075 | 0.41929 | 1.01315 | 0.50030 |
| **Darwin IS** | 0.6 | 91230000 | 110188 | 1356 | 340.3 | 57.2 | 5.7 | 0.00127 | 0.55316 | 1.02306 | 0.45239 |
| **Ecuador IS** | 0.3 | 8620000 | 138730 | 880 | 277.6 | 79.2 | 15.2 | 0.02498 | 2.22774 | 1.13532 | 0.79412 |
| **Espanola** | 3.2 | 50300000 | 144162 | 210 | 42.4 | 25.3 | 2.3 | 0.00077 | 0.42005 | 1.00510 | 0.05071 |
| **Fernandina** | 0.06 | 90850000 | 125312 | 1458 | 346.1 | 80.7 | 8.2 | 0.00389 | 0.93894 | 1.04165 | 0.53344 |
| **Floreana** | 1.9 | 155840000 | 103491 | 568 | 103.4 | 56.8 | 5.0 | 0.00090 | 0.49319 | 1.01176 | 0.15768 |
| **Genovesa** | 0.4 | 7520000 | 140115 | 76 | 12.6 | 41.3 | 4.6 | 0.00167 | 0.66032 | 1.00888 | 0.02784 |
| **Marchena** | 0.4 | 21760000 | 122268 | 299 | 53.7 | 36.0 | 3.5 | 0.00062 | 0.39246 | 1.00608 | 0.07173 |
| **Pinta** | 0.4 | 31050000 | 146342 | 633 | 145.8 | 70.4 | 8.0 | 0.00521 | 1.03896 | 1.04160 | 0.29472 |
| **Pinzon** | 1.5 | 14980000 | 72167 | 455 | 96.5 | 74.7 | 8.4 | 0.00690 | 1.20929 | 1.05444 | 0.27795 |
| **Rabida** | 1.4 | 870000 | 74244 | 349 | 92.2 | 36.7 | 8.6 | 0.00287 | 0.87080 | 1.08403 | 0.27412 |
| **San Cristobal** | 3.2 | 476270000 | 142778 | 718 | 147.6 | 46.8 | 3.5 | 0.00073 | 0.43091 | 1.00706 | 0.19780 |
| **Santa Cruz** | 1.8 | 962120000 | 73208 | 862 | 159.4 | 48.6 | 2.5 | 0.00040 | 0.31745 | 1.00368 | 0.21746 |
| **Santa Fe** | 2.6 | 6340000 | 91066 | 266 | 52.9 | 56.8 | 8.5 | 0.00413 | 1.02071 | 1.03302 | 0.15294 |
| **Santiago** | 0.7 | 376940000 | 79272 | 909 | 199.9 | 71.9 | 4.9 | 0.00099 | 0.49129 | 1.01122 | 0.27041 |
| **Sierra Negra IS** | 0.5 | 720110000 | 92658 | 1123 | 268.4 | 66.3 | 3.6 | 0.00057 | 0.37371 | 1.00567 | 0.33151 |
| **Wolf IS** | 0.5 | 298670000 | 124477 | 1705 | 404.8 | 68.3 | 7.5 | 0.00093 | 0.48133 | 1.02685 | 0.55000 |

Table 2.6: Results for significant models tested. The taxonomic groups are: native plants (NP), native vertebrates (NV), native birds (NB), native mammals (NM), native reptiles (NR), native invertebrates (NI), single island endemic plants (SIEP), single island endemic vertebrates (SIEV), and single island endemic invertebrates (SIEI). HD is habitat diversity, GDM is Log(Area) + Time + Time$^2$, RE is range of elevation, SE is standard deviation of elevation, RS is range of slope, SS is standard deviation of slope, TC is total curvature, SC is standard deviation of curvature, RU is rugosity, and CTCI is compound terrain complexity index. For model outputs, ΔAIC, $R^2$, adjusted $R^2$, and p value are reported. Models that are extensions to the general dynamic model (GDM) have likelihood ratio test (LRT) p values associated with them to compare against the GDM.

| Group | Model | ΔAIC | $R^2$ | Adj $R^2$ | P value | LRT P value |
|---|---|---|---|---|---|---|
| NP | Log(Area) | 4.910 | 0.704 | 0.674 | 0.00064 | |
| | GDM | 0.660 | 0.851 | 0.795 | 0.00113 | |
| | GDM + Isolation | 0 | 0.881 | 0.813 | 0.00239 | 0.15247 |
| | GDM + Isolation + RE | 0.920 | 0.891 | 0.800 | 0.00748 | 0.30322 |
| | GDM + Isolation + SE | 1.313 | 0.887 | 0.794 | 0.00821 | 0.29889 |
| | GDM + Isolation + RS | 1.583 | 0.885 | 0.789 | 0.00876 | 0.08297 |
| | GDM + Isolation + SS | 1.858 | 0.882 | 0.784 | 0.00935 | 0.07860 |
| | GDM + Isolation + TC | 1.413 | 0.886 | 0.792 | 0.00841 | 0.28654 |
| | GDM + Isolation + SC | 1.691 | 0.884 | 0.787 | 0.00899 | 0.21214 |
| | GDM + Isolation + RU | 1.758 | 0.883 | 0.786 | 0.00913 | 0.21531 |
| | GDM + Isolation + CTCI | 1.378 | 0.887 | 0.792 | 0.00834 | 0.26261 |
| SIEP | No significant models | | | | | |
| NV | Log(Area) | 10.32 | 0.480 | 0.428 | 0.01246 | |
| | Isolation | 13.29 | 0.334 | 0.268 | 0.04884 | |
| | HD | 0 | 0.780 | 0.758 | 0.00014 | |
| | GDM | 4.063 | 0.779 | 0.696 | 0.00533 | |
| | GDM + Isolation | 4.759 | 0.802 | 0.688 | 0.01321 | 0.25345 |
| | GDM + Isolation + HD | 4.130 | 0.841 | 0.708 | 0.02192 | 0.13994 |
| | GDM + Isolation + HD + RS | 2.701 | 0.880 | 0.737 | 0.03266 | 0.06122 |
| SIEV | HD | 0 | 0.601 | 0.561 | 0.00305 | |
| NM | HD | 0 | 0.471 | 0.418 | 0.01367 | |
| NR | Log(Area) | 8.245 | 0.432 | 0.375 | 0.02029 | |
| | Isolation | 9.955 | 0.345 | 0.279 | 0.04482 | |
| | HD | 0 | 0.714 | 0.685 | 0.00054 | |
| | GDM | 3.144 | 0.734 | 0.634 | 0.01097 | |

| | | | | | | |
|---|---|---|---|---|---|---|
| | GDM + Isolation | 5.053 | 0.736 | 0.585 | 0.03390 | 0.76284 |
| | | | | | | |
| NB | Log(Area) | 20.19 | 0.589 | 0.548 | 0.00358 | |
| | Isolation | 25.81 | 0.343 | 0.278 | 0.04532 | |
| | HD | 8.248 | 0.848 | 0.833 | 0.00002 | |
| | GDM | 8.167 | 0.892 | 0.851 | 0.00032 | |
| | GDM + Isolation | 0.884 | 0.950 | 0.922 | 0.00012 | 0.00231 |
| | GDM + Isolation + HD | 0 | 0.961 | 0.928 | 0.00038 | 0.00228 |
| | GDM + Isolation + HD + RE | 0.224 | 0.966 | 0.926 | 0.00158 | 0.00298 |
| | GDM + Isolation + HD + SE | 0.275 | 0.966 | 0.925 | 0.00160 | 0.00306 |
| | GDM + Isolation + HD + RS | 1.916 | 0.961 | 0.914 | 0.00223 | 0.00657 |
| | GDM + Isolation + HD + SS | 1.327 | 0.963 | 0.918 | 0.00198 | 0.00500 |
| | GDM + Isolation + HD + TC | 1.784 | 0.961 | 0.915 | 0.00217 | 0.00618 |
| | GDM + Isolation + HD + SC | 1.689 | 0.962 | 0.916 | 0.00213 | 0.00592 |
| | GDM + Isolation + HD + RU | 1.959 | 0.961 | 0.914 | 0.00225 | 0.00670 |
| | GDM + Isolation + HD + CTCI | 1.416 | 0.963 | 0.918 | 0.00201 | 0.00521 |
| | | | | | | |
| NI | Log(Area) | 11.63 | 0.472 | 0.419 | 0.01359 | |
| | HD | 0 | 0.800 | 0.780 | 0.00009 | |
| | GDM | 8.321 | 0.713 | 0.605 | 0.01469 | |
| | GDM + Isolation | 8.274 | 0.758 | 0.619 | 0.02553 | 0.15247 |
| | GDM + Isolation + HD | 5.936 | 0.831 | 0.691 | 0.02574 | 0.04107 |
| | GDM + Isolation + HD + RE | 5.706 | 0.860 | 0.692 | 0.04691 | 0.03488 |
| | GDM + Isolation + HD + RS | 0.126 | 0.912 | 0.806 | 0.01590 | 0.00265 |
| | GDM + Isolation + HD + SS | 4.515 | 0.873 | 0.721 | 0.03736 | 0.02029 |
| | GDM + Isolation + HD + TC | 6.023 | 0.856 | 0.684 | 0.04981 | 0.04023 |
| | GDM + Isolation + HD + SC | 5.104 | 0.867 | 0.707 | 0.04183 | 0.02654 |
| | GDM + Isolation + HD + RU | 5.351 | 0.864 | 0.701 | 0.04385 | 0.02969 |
| | GDM + Isolation + HD + CTCI | 5.487 | 0.862 | 0.697 | 0.04500 | 0.03159 |
| | | | | | | |
| SIEI | HD | 0 | 0.410 | 0.351 | 0.02487 | |
| | | | | | | |
| Snails | Log(Area) | 15.96 | 0.243 | 0.210 | 0.01237 | |
| Full | HD | 0 | 0.600 | 0.583 | 0.00001 | |
| | GDM | 14.53 | 0.390 | 0.303 | 0.01393 | |
| | GDM + Isolation | 14.16 | 0.446 | 0.335 | 0.01499 | 0.12378 |
| | GDM + Isolation + HD | 3.865 | 0.661 | 0.572 | 0.00053 | 0.00065 |
| | GDM + Isolation + HD + RE | 5.557 | 0.665 | 0.553 | 0.00142 | 0.00184 |
| | GDM + Isolation + HD + SE | 5.865 | 0.661 | 0.548 | 0.00157 | 0.00212 |
| | GDM + Isolation + HD + RS | 5.785 | 0.662 | 0.549 | 0.00153 | 0.00205 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | GDM + Isolation + HD + SS | 4.345 | 0.681 | 0.575 | 0.00096 | 0.00104 |
| | GDM + Isolation + HD + TC | 4.489 | 0.679 | 0.572 | 0.00100 | 0.00111 |
| | GDM + Isolation + HD + SC | 4.283 | 0.682 | 0.576 | 0.00094 | 0.00101 |
| | GDM + Isolation + HD + RU | 4.480 | 0.679 | 0.572 | 0.00100 | 0.00111 |
| | GDM + Isolation + HD + CTCI | 4.897 | 0.674 | 0.565 | 0.00115 | 0.00135 |
| | | | | | | |
| Snails | Log(Area) | 12.57 | 0.334 | 0.295 | 0.00949 | |
| NDVI | HD | 3.612 | 0.585 | 0.560 | 0.00014 | |
| | GDM | 3.650 | 0.663 | 0.595 | 0.00078 | |
| | GDM + Isolation | 4.542 | 0.682 | 0.591 | 0.00190 | 0.29245 |
| | GDM + Isolation + HD | 0.404 | 0.770 | 0.681 | 0.00083 | 0.02670 |
| | GDM + Isolation + HD + RE | 1.557 | 0.780 | 0.670 | 0.00210 | 0.04412 |
| | GDM + Isolation + HD + SE | 1.882 | 0.776 | 0.664 | 0.00231 | 0.05105 |
| | GDM + Isolation + HD + RS | 2.271 | 0.771 | 0.657 | 0.00259 | 0.06076 |
| | GDM + Isolation + HD + SS | 1.005 | 0.786 | 0.679 | 0.00179 | 0.03440 |
| | GDM + Isolation + HD + TC | 0.260 | 0.794 | 0.691 | 0.00144 | 0.02453 |
| | GDM + Isolation + HD + SC | 0.849 | 0.788 | 0.682 | 0.00171 | 0.03206 |
| | GDM + Isolation + HD + RU | 0 | 0.797 | 0.696 | 0.00133 | 0.02179 |
| | GDM + Isolation + HD + CTCI | 0.480 | 0.792 | 0.688 | 0.00153 | 0.02711 |

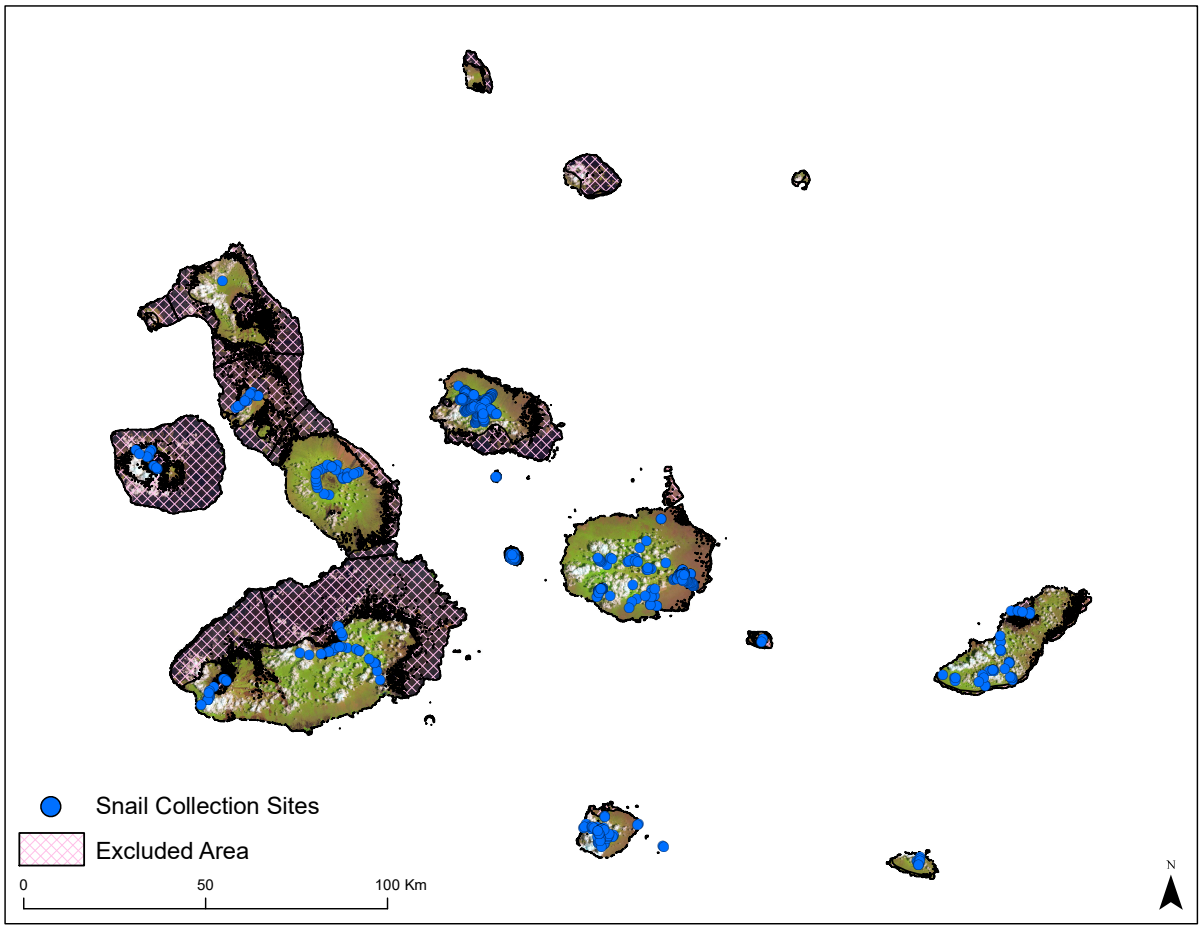


Figure 2.1: Satellite image of Galapagos Islands. The excluded areas (areas with low levels of photosynthesis and considered unsuitable for snails to inhabit) were not incorporated when running the zonal statistic tool for each island to determine the effect of the normalized difference vegetation index (NDVI) on the snail dataset models (see Methods). Not shown on the map are Darwin and Wolf islands located approximately 150 km NW of the northernmost tip of Isabela Island. These two islands were not included in the analyses.

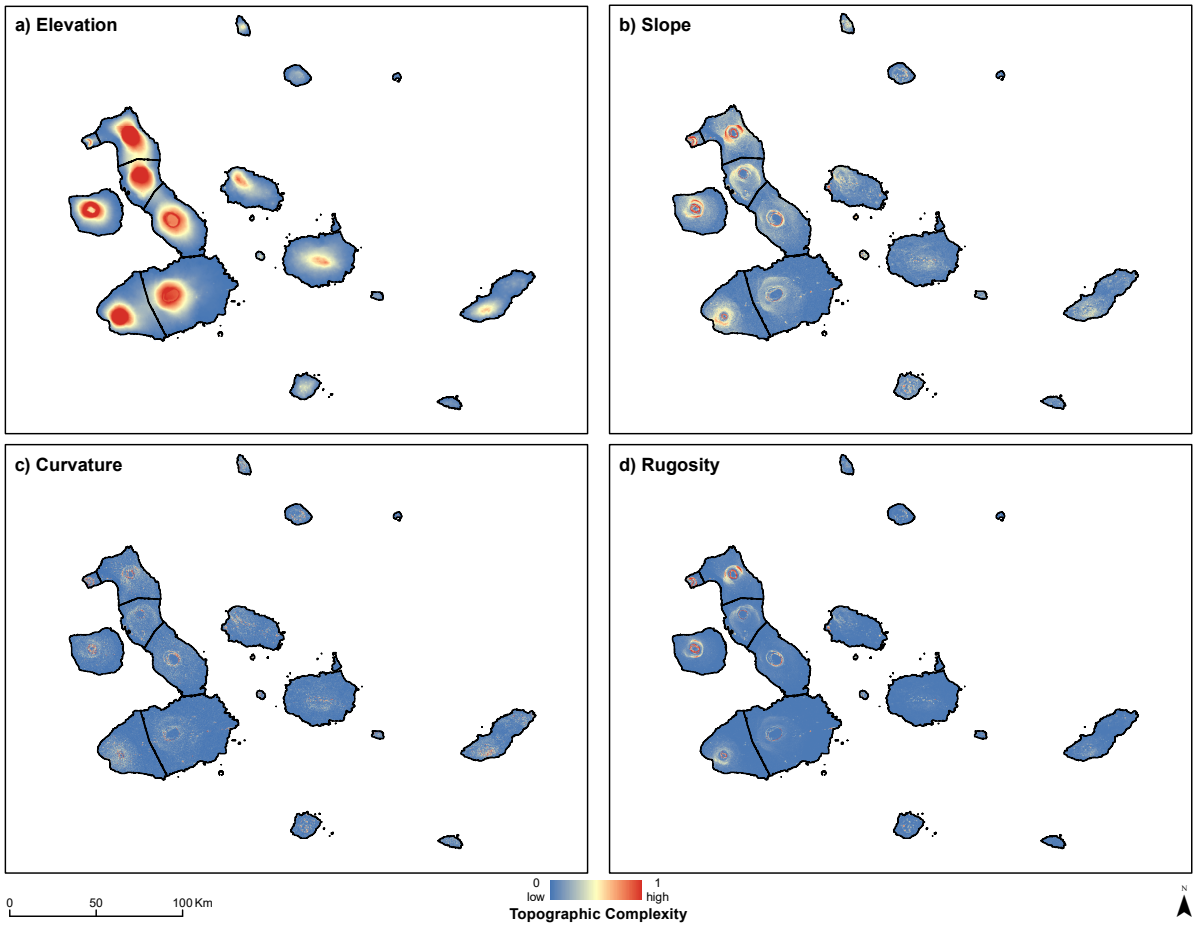


Figure 2.2: Rasters used to compute indices of topographic complexity. Isabela Island is divided into six separate areas, which are considered as separate islands for the snail datasets (see Methods). Because distribution data is not available at the volcano level for the remaining datasets from the Charles Darwin Foundation Datazone, Isabela is considered as a single island for these datasets.

# Chapter 3: Effects of environmental variation on shell morphology and metabolic rate for an endemic terrestrial snail of the Galapagos archipelago

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**Keywords**
metabolic rate, shell morphology, environmental variation, trait diversity, Galapagos, path analysis

**Abstract:**

The effect that environment has on a species' morphology has been well studied in the context of how species diversify. Typically, such studies have focused on the morphological changes whereas less attention has been directed to characterizing potential physiological changes in the same lineages. Determining the link between morphological and physiological changes associated with environmental variation is likely to enhance our understanding of why and how adaptation arise. The endemic land snails of the genus *Naesiotus* form the most species rich adaptive radiation of the Galapagos Islands with over 60 species described. These snails inhabit most islands from low elevations that are hot and arid to higher elevations that are cool and humid. Along this climatic gradient, *Naesiotus* species present a diverse spectrum of shell size, shape, and color. We use path analysis to investigate the relationships between physiology, morphology, and environment. More specifically, we investigate changes in metabolic rate (physiology) and shell shape and size (morphology) among individuals as related to variation in landscape and climate (environment) where species occur. We find that, using cloud cover and shell shape as proxies for climate and morphology, respectively, climate has a significant positive effect on physiology whereas morphology has a significant negative effect on physiology.

## Introduction:

Species can adapt to their changing environment in multiple ways resulting in phenotypic variation. This variation can be due to morphological or physiological changes in species. When phenotypic change is associated with environmental change (resulting in a

phenotypic-environment association), species could have adapted to their habitats morphologically, physiologically, or both. Most studies have focused on morphological or physiological adaptation independently. Specifically, many studies have focused on the variation in morphological characteristics due to habitat (e.g., Galapagos finches [Grant and Grant 2014], Cichlid fishes [Muschick et al. 2012], Anole lizards [Losos and Ricklefs 2009]). However, change in morphology could impact physiology, and vice versa. To withstand a changing environment, species can move away from the environment, go extinct locally, or adapt to the changing environment. Adaptations are crucial, particularly for sessile species that are unable to readily move to avoid suboptimal environmental conditions.

Plants are often used to determine how environmental conditions might affect simultaneously the morphology and physiology of organisms. For instance, to regulate water balance through transpiration in plants, the stomata can either open or close (Ku et al. 1977). During times when the stomata are closed, photosynthesis slows due to the lower levels of carbon dioxide (Farquhar and Sharkey 1982), which affects the growth rate of the plant. In this example, the alteration of the morphology of stomata in response to environmental conditions is changing the physiology of the plant by altering the chemical balance. In areas with high salt concentrations, studies have shown a wide range of adaptations for plants to become salt-resistant by either altering morphological characteristics (Rozema et al. 1982; Rozema et al. 1985), physiological characteristics (De Jong 1979; Stewart et al. 1979), or both (Rozema et al. 1982; Hesp 1991).

Other species, especially intertidal or marine species, have adapted to withstand water fluctuations or limited light. Intertidal mussels that experience a wide range of temperature, salinity concentrations, and water flow, have many morphological and physiological adaptations. Some mussel species in the genus *Modiolus*, have altered the primary excretory product to withstand the fluctuations in intertidal habitats to handle nitrogen catabolism (Needham 1935). Ribbed shells and the size of the shell in mussels have been shown to shift depending on the what region of the intertidal zone the mussel inhabits (Lent 1969) and the temperature of the water (Lent 1968), respectively. Many coral species have adapted to areas with rapid flows of water (Vogel 1984) and limited light (Falkowski and Dubinsky 1981).

Land snails are another group of organisms that adapt to environmental variation as a result of their limited mobility. Land snails along environmental gradients are known to

exhibit diverse shell sizes and shapes (Coppois and Glowacki 1983; Gould 1984; Goodfriend 1986; Parent 2008). Shell morphology is likely important for many different aspects of snail survival. Shells provide protection against predation (Goodfriend 1986), prevent water loss (Machin 1967; Goodfriend 1986), and dissipate heat to avoid desiccation (McMahon 1990). Along with morphological adaptations to the environment, land snails can estivate to withstand long periods of drought or unfavorable conditions.

The genus *Naesiotus*, a morphologically diverse group of endemic land snails from the Galapagos Islands (Parent and Crespi 2009), represent the most species rich adaptive radiation of the Galapagos with over 60 species currently described (Parent and Crespi 2006). *Naesiotus* inhabits most islands in the Galapagos from lower elevations that are hot and arid to higher elevations that are cool and humid. Previous studies have shown that *Naesiotus* species tend to have a more elongated shell shape in more arid environments and a rounder shell shape in more humid environments (Parent 2012). This phenotypic-environment association suggests that snails with different shell shape have adapted to different habitats. However, morphological adaptation is likely to be associated with a difference in metabolic costs, potentially related to building and maintaining the snail's shell. The link between morphological and physiological variation and their potential interaction with microhabitat might play an important role in how lineages diversify.

During estivation, land snail's metabolic rate has been found to be 10-30% of their normal resting metabolic rate (Herreid 1977; Vorhaben et al. 1984; Barnhart and McMahon 1987). The large variation in metabolic rate during estivation is most likely do to morphological differences between snail shells and the location that these snails were sampled. In this study, we investigated the variation seen in metabolic rate to determine how morphology and environment are affecting the metabolic rate in *Naesiotus*. We tested the relationships between metabolic rate (physiology), shell shape and size (morphology), and climate and landscape (environment) of where *Naesiotus* were collected. In areas with more arid environments, we expected snail shells to be smaller in size, larger in shape (more elongated shells), and have a lower metabolic rate. Adapting to the environment by having a smaller and elongated shell and a lower metabolic rate, water would be conserved which is a larger issue for snails in drier environments. By understanding the physiological and

morphological variations occurring between populations in different environments, we will further our knowledge on why and how species adapt.

**Materials and Methods:**

*Field Collection*

Adult *Naesiotus* snails were collected from 22 locations on three Galapagos islands during two field seasons (August 2015 and May-July 2016) (Figure 3.1). A total of 437 individuals from 15 species were collected with some species being collected from multiple populations (Table 3.1). Two transects on Santa Cruz Island (referred to as Garrapatero and El Chato) were surveyed where two and eight collection sites were examined, respectively. One population from a species found at El Chato was found at La Cascada, a location near sea level on the outskirt of the town of Puerto Ayora, on Santa Cruz Island. Two volcanos on Isabela Island were sampled. On Volcano Sierra Negra, three transects were sampled for a total of eight collection sites. On Volcano Alcedo, snails were collected on the eastern slope and on the southern rim of the volcano. On Floreana Island, one location was sampled in the highlands at Cerro Pajas. After collections in the field, snails were transported to the towns on each island for the physiological and morphological measurements.

*Physiological Measurements*

All metabolic measurements on individual snails were performed using oxygen and carbon dioxide analyzers (FOXBOX, Sable Systems International, Las Vegas, NV) and water vapor analyzer (RH-300, Sable Systems International). The equipment was calibrated using air drawn from a 1-gallon container to eliminate fluctuations in airflow and allow for a more consistent air composition (e.g., oxygen percentage). The air was scrubbed of water and carbon dioxide during calibration by using a drierite-ascarite-drierite column, which was removed before data collection. During data collection, the flow rate was controlled by an internal pump set to 200 mL/min. Data were recorded using Expedata and Daemon software (Sable Systems International).

Prior to data collection, each snail was fasted for 24 to 48 hours to account for a post-absorptive state, which occurs right after completing digestion causing the normal metabolic rate to shift. To measure metabolic activity, each snail was placed and sealed in a 50 mL

syringe previously purged with calibrated air for 2 minutes. After 80 minutes, a 25 mL sample of air from the syringe was injected into the FOXBOX. The injected air samples were used to measure rate of oxygen consumption ($VO_2$, mL/min), rate of carbon dioxide production ($VCO_2$, mL/min), and water vapor pressure (WVP, kPa).

*Morphological Measurements*

The shell height and width and aperture (i.e., the shell opening) length and width were recorded for all snails collected for metabolic measurements. Shell volume was estimated as a cone (using shell height and width) and aperture surface area was estimated as an oval (using aperture height and width). Shell shape was calculated by using the ratio of shell length to shell width.

*Climate and Landscape Measurements*

The 19 bioclimatic variables from the WorldClim dataset (Hijmans et al. 2005) were used as different measures of the climate. This dataset had a spatial resolution of 1-kilometer cells and was downloaded for the Galapagos Islands. Bioclimatic variable 4 (bio 4) was the only WorldClim variable used. Bio 4 is a measure of temperature seasonality which looks at temperature change over the course of the year. All of the bioclimatic variables, except for bio 3, 4, and 7, were highly correlated with elevation thus they were not used. Both bio 3 and 7, measures of isothermality and annual temperature range, respectively, are calculated from other bioclimatic variables, thus they were disregarded since the variables used to calculate bio 3 and 7 are highly correlated with elevation.

Another measure used to determine climate of an area was a variable we called cloud cover. This was generated by downloading a year's worth (total of 24 images) of Landsat 8 level-1 product from the USGS EarthExplorer (USGS 2016) for Galapagos. The images had a spatial resolution of 30-meter cells. The 24 images were reclassified so all cells that included clouds were equal to 1 and all non-cloud cells were equal to 0. By overlaying these images in Esri's ArcMap 10.3.1 and using the raster calculator tool, a single raster with values ranging from 0 to 24 was created. This raster was used as a proxy to indicated the amount of cloud cover that every cell in Galapagos experienced for the year (Figure 3.1).

Elevation and slope were used to measure variation in landscape. The digital elevation model (DEM) was downloaded from USGS Global Data Explorer using the NASA Shuttle Radar Topography Mission (SRTM) 1 arc-sec data (NASA 2013). The 30-meter resolution DEM was used to create a slope raster in ArcMap.

*Statistical Analysis*

The relationships between physiology, morphology, and the environment were tested with path analysis in SPSS Amos Graphics 24.0. A path analysis using maximum likelihood was utilized to determine the direct and indirect effect that each variable had on the rest of the variables. Physiology and morphology were explained using latent variables (unobserved variables being explained by multiple observed variables) with metabolic rate representing physiology and shell size and shape representing morphology. Environment was divided into two latent variables: climate and landscape.

The hypothesized relationship between all of the latent variables is shown in Figure 3.2 (referred to as the full model). For the full model, the observed variables for the metabolic rate latent variable were $VO_2$, $VCO_2$, and WVP; the observed variables for the morphology latent variable were shell volume, shell shape, and aperture surface area; the observed variables for the climate latent variable were bio 4 and cloud cover; and the observed variables for the landscape latent variable were elevation and slope. Since the full model did not pass the chi-squared or the root mean square error approximation (RMSEA) goodness of fit, simpler models were derived. To get the simpler models, models were created that kept the metabolic rate latent variable but simplified how morphology and environment were represented in the model. All combinations of the observed variables for morphology and environment were tested. The simplest model created that passed the goodness of fit tests (chi squared and RMSEA) and retained the overall relationships of interest between physiology, morphology, and environment, was used to access the effects of each of these relationships. For the simplest model used (Figure 3.3), landscape was not accounted for and shell shape was used as a proxy for morphology and cloud cover was used as a proxy for climate. The standardized direct and indirect effects for the simple model were recorded from the Amos output.

**Results:**

The full model did not pass the chi-squared or the root mean square error of approximation (RMSEA) model fit tests. The chi-square test indicated that the model had a p value less than 0.001, stating that the model was unacceptable for the data (Arbuckle 2016). The RMSEA test was 0.18 and for the model to have a good fit, the value should be below 0.05 (MacCallum et al. 1996). The simple model did pass the chi-squared and the RMSEA model fit tests. The chi-square test indicated that the model had a p value greater than 0.05 (p value = 0.759), thus the simple model was acceptable for the data (Arbuckle 2016). The RMSEA had a value less than 0.001, meaning that the simple model was a good fit for this data.

With the full model not being a good fit, the simple model removed the variables associated with landscape and kept only shell shape as the only morphology variable and cloud cover as the only climate variable. All of the direct effects and p values are in Table 3.2 and the indirect effects are in Table 3.3 for the simple model. Cloud cover had a significant positive direct effect on shell shape and metabolic rate and a positive indirect effect on all three observed variables under metabolic rate. Thus, elongated shell shapes and elevated metabolic rates are found associated with habitats with greater yearly cloud cover. Shell shape had a significant negative direct effect on metabolic rate and a negative indirect effect on all three variables under metabolic rate. As shells become more elongated, the snail's metabolic rate decreases. Metabolic rate had a significant positive direct effect on oxygen consumption and carbon dioxide production but had a significant negative direct effect on water loss. Oxygen consumption had a significant positive direct effect on water loss and although there was not a significant effect on carbon dioxide production, the direct effect was negative.

**Discussion:**

*WorldClim Data*

The use of global bioclimatic datasets has become increasingly popular in ecological studies with the development of WorldClim in 2005 (Hijmans et al. 2005). The dataset from WorldClim is interpolated from weather stations to get the different variables associated with temperature and precipitation. For areas that have a sparse distribution of weather stations in the area, such as archipelagos, the uncertainty is going to be much higher. Latitude, longitude,

and elevation of weather stations are used as independent variables when the WorldClim climate layers are created thus most of the bioclimatic variables were highly correlated with elevation for the Galapagos. With the combination of the Galapagos Islands having a range of elevation from 0 to 1,705 meters and few weather stations, especially on Isabela with the largest range of elevation, the uncertainty of this dataset for Galapagos is going to be high. The dataset had temperature and precipitation being the same around the volcanos even though the cloud cover (Figure 3.1) is not evenly distributed with elevation due to prevailing winds coming from the southeast. In regions on the back side of the volcanos from the prevailing winds, the WorldClim dataset does not seem to have accurate recordings.

*Latent Variables and Categorical Data*

In the model, the latent variables metabolic rate, morphology, climate, and landscape were highly variable depending on what observed variables were being described by the latent variables. This had a huge impact on the outcome in the full model since morphology, climate, and landscape were only broken down into no more than three observed variables. Deciding what observed variables to use to describe the variation that is seen in climate and landscape could change the results from the path analysis. The climate variables used were seasonality and cloud cover but this does not directly take average annual temperature and precipitation into effect or use the other 18 bioclimatic variables available through WorldClim. Climate in the model is measuring climate at a large scale but the climate at the microhabitat scale might be more important in determining the relationship between climate and metabolic rate or morphology. Landscape, which is known to be highly variable and the complexity of landscape can be measured in multiple ways, was only quantified using two variables. Although elevation and slope are two common ways to view variation across a landscape, other components of the landscape are important to consider that affect the climate. Aspect, which is the direction that the slope is facing, affects the climate at a specific location since the location might be facing towards or away from prevailing winds or might receive more radiation from the sun if facing certain directions.

The cloud cover variable was created as a way to determine climate that would be relevant for the snail populations. Although temperatures might have been interpolated to be high for a location from the WorldClim dataset, if there is persistent cloud cover, the actual

temperature at the microhabitat level could be different. With an interest in the differences between snail populations in areas that are considered arid and humid but not having a clear distinction between the two regions, cloud cover was one way to make this distinction. Reduced cloud cover can result from acidification and with decreased cloud cover, evapotranspiration will be higher (Guthrie 2001). For snails in an arid environment, desiccation is going to be a bigger problem thus adaptations to combat this problem would arise. Cloud cover has been used before in other another studies that demonstrated that body temperature was on average lower but had a higher variation on cloudy days than on clear skies (Gibson and Falls 1979; Andrews 1998).

Due to limitations with the program used, random effects were not taken into consideration for species or locations sampled. By not taking into account that the variation observed in metabolic rate or morphology might solely be due to interspecific variation, the relationship between metabolic rate and morphology might be different for different species. With certain species having a larger number of individuals measured than other species, the effect that each of the latent variables have on each other is going to be strongly influenced by the species that have a higher sample size.

*Model Relationships*

A negative relationship was identified between shell shape, which is used as proxy for morphology, and metabolic rate. For snails that have a larger shell shape, the body size is going to be smaller than a snail with a smaller shell shape. A large shell shape indicates a shell is much longer than it is wide so the shell is going to be elongated and skinny which would result in a smaller body size compared to a round shell that has the same volume. Although body size was not directly measured, the shell shape should be a good indicator of body size for these snails. Thus, as the shell shape decreases, the body size of a snail increases which would increase the metabolic rate. This has been observed in many previous studies since Kleiber (1932) which stated that as body size increases, metabolism is going to increase as well.

With a positive relationship between climate and metabolic rate, as cloud cover increases so does metabolic rate which might indicate that since there is less solar radiation, there is going to be less strict regulation on metabolism due to desiccation not being as big of

an issue. Cloud cover also had a positive relationship with shell shape, indicating that elongated shells are found in areas with more cloud cover. Through these relationships, climate has a positive effect on metabolic rate and morphology but morphology has a negative effect on metabolic rate. The effect that climate has on metabolic rate is stronger than the effect that morphology has on metabolic rate. This might indicate that while shell morphology is important, the relationship between climate and metabolic rate is more important. Thus, the habitat that a snail is found has a larger impact on the metabolic rate than the shell morphology.

**Conclusions:**

The use of path analysis to determine the relationships between physiology, morphology, and environment is a clear way to examine the direct and indirect effects of these relationships. However, the use of latent variables to describe these relationship is difficult since there are many different ways that physiology, morphology, and environment can be quantified. Since the observed variables under each latent variable changes the relationship between the latent variables in the hypothesized model, further work needs to be done to ensure that the latent variables, mainly climate, are standardized in a way that can be replicated for future studies.

Table 3.1: Description of where *Naesiotus* species were collected for metabolic rate and shell morphology measurements with the number (N) of individuals measured per species.

| **Species** | **Island** | **Transect** | **N** |
|---|---|---|---|
| *N. akamatus* | Santa Cruz | Garrapatero | 18 |
| *N. albermarlensis* | Isabela | Sierra Negra | 48 |
| *N. hirsutus* | Santa Cruz | Garrapatero | 11 |
| *N. nesioticus* | Santa Cruz | Chato | 60 |
| *N. nux* | Floreana | Pajas | 14 |
| *N. reibischi* | Santa Cruz | Garrapatero | 7 |
| *N. simrothi* | Isabela | Sierra Negra | 8 |
| *N. tortuganus* | Isabela | Sierra Negra | 38 |
| *N. unifasciatus* | Floreana | Pajas | 16 |
| *N. wolfi* | Santa Cruz | Chato | 93 |
| *N. sp 1* | Santa Cruz | Chato | 79 |
| *N. sp 2* | Santa Cruz | Garrapatero | 6 |
| *N. sp 3* | Isabela | Alcedo | 17 |
| *N. sp 4* | Isabela | Alcedo | 14 |
| *N. sp 5* | Isabela | Sierra Negra | 8 |

Table 3.2: Results from simple model path analysis showing the standardized regression estimates as the direct effects. Significant relationships are indicated with an asterisks (* P value < 0.05; ** P value < 0.01; *** P value < 0.001). Metabolic rate is italicized to indicate it is a latent variable. The metabolic rate variables, $VCO_2$, $VO_2$, and WVP, stand for rate of carbon dioxide production, rate of oxygen consumption, and rate of water vapor produced, respectively.

| **Response** | **Explanatory** | **Direct Effect** | **P Value** |
|---|---|---|---|
| *Metabolic Rate* | Cloud Cover | 0.2866 | *** |
| *Metabolic Rate* | Shell Shape | -0.1916 | ** |
| VO2 | *Metabolic Rate* | 0.7846 | *** |
| VCO2 | *Metabolic Rate* | 0.9484 | *** |
| VCO2 | VO2 | -0.3570 | |
| WVP | *Metabolic Rate* | -0.7185 | *** |
| WVP | VO2 | 1.4726 | *** |
| Shell Shape | Cloud Cover | 0.1376 | ** |

Table 3.3: Results from simple model path analysis showing the standardized indirect effects. Metabolic rate is italicized to indicate it is a latent variable. The metabolic rate variables, $VCO_2$, $VO_2$, and WVP, stand for rate of carbon dioxide production, rate of oxygen consumption, and rate of water vapor produced, respectively.

| **Response** | **Explanatory** | **Indirect Effect** |
|---|---|---|
| VO2 | Cloud Cover | 0.2042 |
| VO2 | Shell Shape | -0.1503 |
| VCO2 | Cloud Cover | 0.1740 |
| VCO2 | Shell Shape | -0.1280 |
| WVP | Cloud Cover | 0.1137 |
| WVP | Shell Shape | -0.0837 |

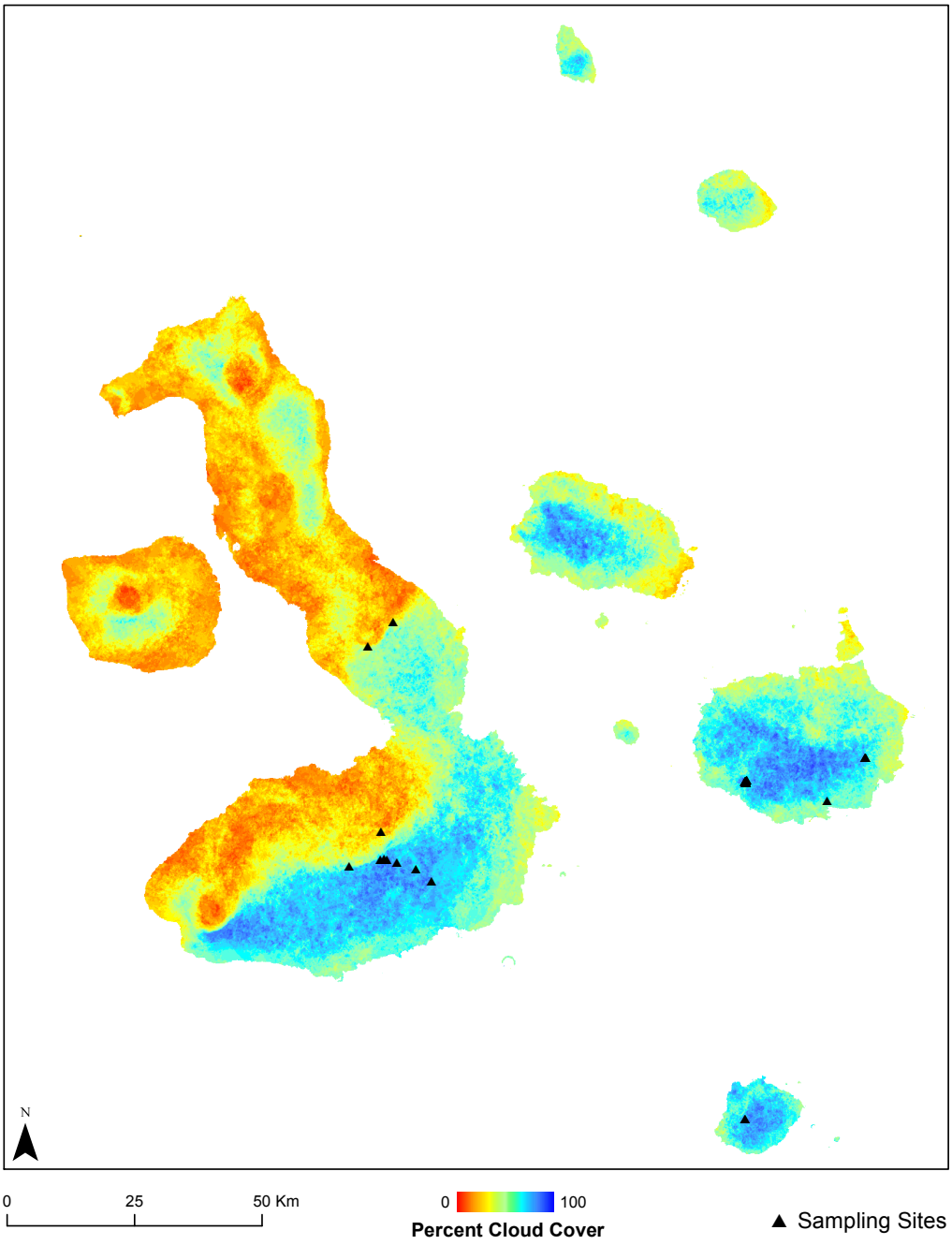


Figure 3.1: Cloud cover of central and western islands of Galapagos for 2016 and the *Naesiotus* sampling locations. The cloud cover percentage was created from a year's worth of satellite imagery from Landsat 8 for a total of 24 images. Areas that had clouds in an image were given a 1 and all other areas were given a 0. Cloud cover was not calculated for the eastern islands of the archipelago because those islands are not on the same satellite path as the central and western islands. Since no sampling sites were on the eastern islands, cloud cover was not calculated. Sampling locations were all populations that metabolic data was collected between 2015 and 2016. Missing from the map are Espanola, San Cristobal, Genovesa, Darwin, and Wolf islands where no snails were collected for this study.

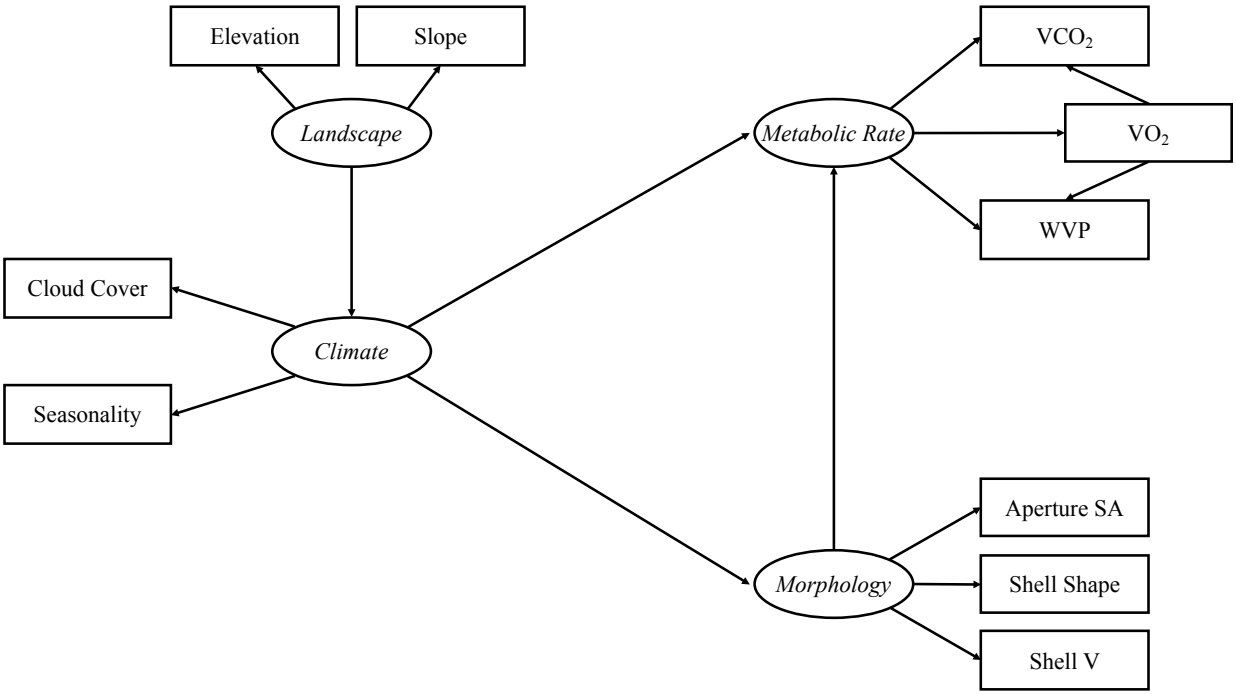


Figure 3.2: Full model for path analysis. Latent variables are italicized and in ovals while observed variables are in rectangles. The metabolic rate variables, $VCO_2$, $VO_2$, and WVP, stand for rate of carbon dioxide production, rate of oxygen consumption, and rate of water vapor produced, respectively. Surface area and volume are represented by SA and V, respectively. Seasonality in the climate latent variable is bioclimatic variable 4 from the WorldClim data.

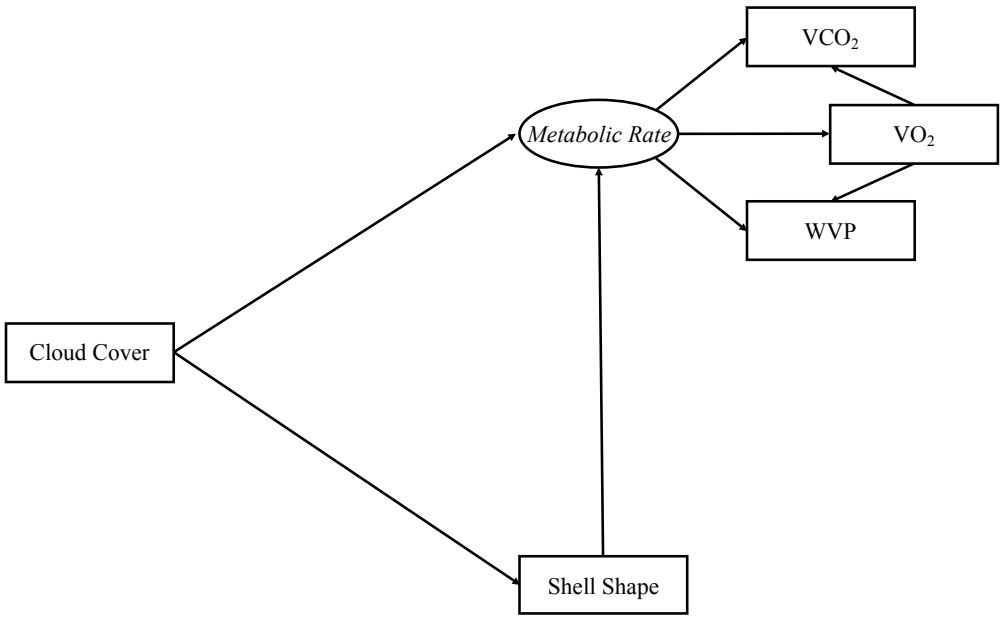


Figure 3.3: Simple model for path analysis. Metabolic rate is italicized and in an oval to indicate it is a latent variable while observed variables are in rectangles. The metabolic rate variables, $VCO_2$, $VO_2$, and WVP, stand for rate of carbon dioxide production, rate of oxygen consumption, and rate of water vapor produced, respectively.

**References:**

Andrews, R.M. (1998). Geographic variation in field body temperature of sceloporus lizards. Journal of Thermal Biology, 23, 329-334.

Arbuckle, J.L. (2016) Amos (Version 24.0), Computer Program and User Guide. Chicago: IBM SPSS.

Barnhart, M.C. and McMahon, B.R. (1987). Discontinuous carbon dioxide release and metabolic depression in dormant land snails. Journal of Experimental Biology, 128, 123-138.

Borregaard, M.K., Amorim, I.R., Borges, P.A.V., Cabral, J.S., Fernandez-Palacios, J.M., Field, R., Heaney, L.R., Kreft, H., Matthews, T.J., Olesen, J.M., Price, J., Rigal, F., Steinbauer, M.J., Triantis, K.A., Valente, L., Weigelt, P., and Whittaker, R.J. (2017). Oceanic island biogeography through the lens of the general dynamic model: assessment and prospect. Biological Reviews, 92, 830-853.

Bro-Jorgensen, J., Brown, M.E., and Pettorelli, N. (2008). Using the satellite-derived normalized difference vegetation index (NDVI) to explain ranging patterns in a lek-breeding antelope: the importance of scale. Oecologia, 158(1), 177-182.

Bungartz, F., Herrera, H.W., Jaramillo, P. Tirado, N., Jimenez-Uzcategui, G., Ruiz, D., Guezou, A., and Ziemmeck, F. (eds.) (2009). Charles Darwin Foundation Galapagos species checklist. Charles Darwin Foundation, Puerto Ayora, Galapagos.

Bunnefeld, N. and Phillimore, A.B. (2012). Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. Ecography, 35, 15-22.

Cameron, R.A.D., Triantis, K.A., Parent, C.E., Guilhaumon, F., Alonso, M.R., Ibanez, M., De Frias Martins, A.M., Ladle, R.J., and Whittaker, R.J. (2013). Snails on oceanic islands: testing the general dynamic model of oceanic island biogeography using linear mixed effect models. Journal of Biogeography, 40, 117-130.

Cardoso, P., Arnedo, M.A., Triantis, K.A., and Borges, P.A.V. (2010). Drivers of diversity in Macaronesian spiders and the role of species extinctions. Journal of Biogeography, 37, 1034-1046.

Chapman, M.G. and Underwood, A.J. (1994). Dispersal of the intertidal snail, Nodilittorina pyramidalis, in response to the topographic complexity of the substratum. Journal of Experimental Marine Biology and Ecology, 179, 145-169.

Coppois, G. and Glowacki, C. (1983). Bulimulid land snails from the Galapagos: 1. Factor analysis of Santa Cruz Island Species. Malacologia, 23, 209-219.

Darwin, C.R. (1859). On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. London, UK: John Murray.

De Jong, T.M. (1979). Water and salinity relations of California beach species. Journal of Ecology, 67, 647-663.

Dimitrov, D., Arnedo, M.A., and Ribera, C. (2008). Colonization and diversification of the spider genus Pholcus Walckenaer, 1805 (Araneae, Pholcidae) in the Macaronesian archipelagos: evidence for long-term occupancy yet rapid recent speciation. Molecular Phylogenetics and Evolution, 48, 596-614.

Durant, J.M., Hjermann, D.O., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N., and Stenseth, N.C. (2005). Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecology Letters, 8(9), 952-958.

Evans, K.L., Newson, S.E., Storch, D., Greenwood, J.J., and Gaston, K.J. (2008). Spatial scale, abundance and the species-energy relationship in British birds. Journal of Animal Ecology, 77(2), 395-405.

Everson, D.A. and Boucher, D.H. (1998). Tree species-richness and topographic complexity along the riparian edge of the Potomac River. Forest Ecology and Management, 109, 305-314.

Falkowski, F.G. and Dubinsky, Z. (1981). Light-shade adaptation of Stylopgora pistillata, a hermatypic coral from the Gulf of Eilat. Nature, 289, 172-174.

Farquhar, G.D. and Sharkey, T.D. (1982). Stomatal conductance and photosynthesis. Annual Review of Plant Physiology, 33(1), 317-345.

Gao, J. (1997). Resolution and accuracy of terrain representation by grid DEMs at a micro-scale. International Journal of Geographic Information Science, 11, 199-212.

Geist, D. (1996). On the emergence and submergence of the Galapagos Islands. Noticias de Galapagos, 56, 5-9.

Geist, D.J., Snell, H., Snell, H., Goddard, C., and Kurz, M. (2014). A paleogeographic model of the Galapagos Islands and biogeographical and evolutionary implications. In The Galapagos: a natural laboratory for the Earth Sciences (pp. 145-166). American Geophysical Union.

Gibson, A.R. and Falls, J.B. (1979). Thermal biology of the common garter snake Thamnophis sirtalis: temporal variation, environmental effects and sex differences. Oecologia, 43, 79-97.

Goodfriend, G.A. (1986). Variation in land-snail shell form and size and its causes: a review. Systematic Biology, 35(2), 204-223.

Gosz, J.R. and Sharpe, P.J.H. (1989). Broad-scale concepts for interactions of climate, topography, and biota at biome transitions. Landscape Ecology, 3(3), 229-243.

Gould, S.J. (1984). Covariance sets and ordered geographic variation in Cerion from Aruba, Bonaire and Curacao: a way of studying nonadaptation. Systematic Zoology, 33(2), 217-237.

Grant, P.R. (1999). Ecology and evolution of Darwin's Finches. Princeton University Press.

Grant, P.R., and Boag, P.T. (1980). Rainfall on the Galapagos and the demography of Darwin's Finches. Auk, 97(2), 227-244.

Grant, P.R. and Grant, B.R. (2008). How and why species multiply: the radiation of Darwin's finches. Princeton University Press.

Grant, P.R. and Grant, B.R. (2014). 40 years of evolution: Darwin's finches on Daphne Major Island. Princeton University Press.

Guthrie, R.D. (2001). Origin and causes of the mammoth steppe: a story of cloud cover, wooly mammoth tooth pits, buckles, and inside-out Beringia. Quaternary Science Review, 20, 549-574.

Havran, J.C., Sytsma, K.J., and Ballard, H.E. (2009). Evolutionary relationships, interisland biogeography, and molecular evolution in the Hawaiian violets (Viola: Violaceae). American Journal of Botany, 96, 2087-2099.

Heaney, L.R. (2000). Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. Global Ecology and Biogeography, 9, 59-74.

Herreid, C.F. (1977). Metabolism of land snails (Otala lacteal) during dormancy, arousal, and activity. Comparative Biochemistry and Physiology Part A: Physiology, 56(2), 211-215.

Hesp, P.A. (1991). Ecological processes and plant adaptations on coastal dunes. Journal of Arid Environments, 21, 165-191.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25, 1965-1978.

Jackson, T.A. (2013). A review of volcanic island evolution and magma production rate: an example from a Cenozoic island arc in the Caribbean. Journal of the Geological Society, 170(6), 547-556.

Jenness, J.S. (2013). Manual: DEM surface tools for ArcGIS. Jenness Enterprises, http://www.jennessent.com/arcgis/surface_area.htm.

Kleiber, M. (1932). Body size and metabolism. Hilgardia, 6, 315-351.

Ku, S., Edwards, G.E., and Tanner, C.B. (1977). Effects of light, carbon dioxide, and temperature on photosynthesis, oxygen inhibition of photosynthesis, and transpiration in Solanum tuberosum. Plant Physiology, 59, 868-872.

Lent, C.M. (1968). Air-gaping by the ribbed mussel, Modiolus demissus (Dillwyn): effects and adaptive significance. Biological Bulletin, 134, 60-73.

Lent, C.M. (1969). Adaptations of the ribbed mussel, Modiolus demissus (Dillwyn), to the intertidal habitat. American Zoologist, 9, 283-292.

Losos, J.B. and Ricklefs, R.E. (2009). Adaptation and diversification on islands. Nature, 457, 830-836.

Lu, H., Liu, X., and Bian, L. (2007). Terrain complexity: definition, index, and DEM resolution. Geoinformatics 2007: Geospatial Information Science, 6753, 231-242.

MacArthur, R.H. and Wilson, E.O. (1963). An equilibrium theory on insular zoogeography. Evolution, 17, 373-387.

MacArthur, R.H. and Wilson, E.O. (1967). The theory of island biogeography. Princeton University Press.

MacCallum, R.C., Browne, M.W., and Sugawara, H.M. (1996). Power analysis and determination of sample size for covariance structure modeling. Psychological Methods, 1, 130-149.

Machin, J. (1967). Structural adaptation for reducing water-loss in three species of terrestrial snail. Journal of Zoology, 152(1), 55-65.

McMahon, R.F. (1990). Thermal tolerance, evaporative water loss, air-water oxygen consumption and zonation of intertidal prosobranchs: a new synthesis. In Progress in Littorinid and Muricid Biology (pp. 241-260). Springer Netherlands.

Muschick, M., Indermaur, A., and Salzburger, W. (2012). Convergent evolution within an adaptive radiation of cichlid fishes. Current Biology, 22, 2362-2368.

NASA J.P.L. (2013). NASA Shuttle Radar Topography Mission Global 1 Arc Second. NASA LP DAAC, https://gdex.cr.usgs.gov/gdex/.

Needham, J. (1935). Problems of nitrogen catabolism in invertebrates: II. Correlation between uricotelic metabolism and habitat in the phylum Mollusca. Biochemical Journal, 29, 238-251.

Otto, R., Whittaker, R.J., Von Gaisberg, M., Stierstorfer, C., Naranjo-Cigala, A., Steinbauer, M.J., Borregaard, M.K., Arevalo, J.R., Garzon-Machado, V., Del Arco, M.J., and Fernandez-Palacios, J.M. (2016). Transferring and implementing the general dynamic model of oceanic island biogeography at the scale of island fragments: the role of geological age and topography in plant diversification in the Canaries. Journal of Biogeography, 43, 911-922.

Parent, C.E. (2008). Diversification on islands: Bulimulid land snails of Galapagos. Ph.D. Thesis, Simon Fraser University, British Columbia, Canada.

Parent, C.E. (2012). Biogeographical and ecological determinants of land snail diversification on islands. American Malacological Bulletin, 30(1), 207-215.

Parent, C.E., Caccone, A., and Petren, K. (2008). Colonization and diversification of Galapagos terrestrial fauna: a phylogenetic and biogeographical synthesis. Philosophical Transactions of the Royal Society B: Biological Sciences, 363(1508), 3347-3361.

Parent, C.E. and Crespi, B.J. (2006). Sequential colonization and diversification of Galapagos endemic land snail genus Bulimulus (Gastropoda, Stylommatophora). Evolution, 60(11), 2311-2328.

Parent, C.E. and Crespi, B.J. (2009). Ecological opportunity in adaptive radiation of Galapagos endemic land snails. The American Naturalist, 174(6), 898-905.

Paulay, G. (1994). Biodiversity on oceanic islands: its origin and extinction. American Zoologist, 34(1), 134-144.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J, and Stenseth, N.C. (2005). Using the satellite-derived NDVI to access ecological responses to environmental change. Trends in Ecology and Evolution, 20(9), 503-510.

Pettorelli, N., Ryan, S. Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., and Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research, 46, 15-27.

Richerson, P.J. and Lum, K. (1980). Patterns of plant species diversity in California: relation to weather and topography. The American Naturalist, 116(4), 504-536.

Ricklefs, C.L. and Bermingham, E. (2004). Application of Johnson et al.'s speciation threshold model to apparent colonization times of island biotas. Evolution, 58, 1664-1673.

Rigal, F., Whittaker, R.J., Triantis, K.A., and Borges, P.A.V. (2013). Integration of non-indigenous species within the interspecific abundance-occupancy relationship. Acta Oecologica, 48, 69-75.

Rouse, J.W., Haas, R.H., Schell, J.A., and Deering, D.W. (1974). Monitoring vegetation systems in the Great Plains with ERTS. Third Earth Resources Technology Satellite-1 Symposium, NASA, Washington, D.C.

Rozema, J., Bijl, F., Dueck, T., and Wesselman, H. (1982). Salt-spray stimulated growth in strandline species. Physiologia Plantarum, 56, 204-210.

Rozema, J., Biljwaard, P., Prast, B., and Broekman, R. (1985). Ecophysiological adaptations of coastal halophytes from foredunes and salt marshes. Vegetatio, 62, 499-521.

Ruggiero, A. and Hawkins, B.A. (2008). Why do mountains support so many species of birds? Ecography, 31(3), 306-315.

Snell, H.M., Stone, P.A., and Snell, H.L. (1996). A summary of geographic characteristics of the Galapagos Islands. Journal of Biogeography, 23(5), 619-624.

Stein, A., Gerstner, K., and Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters, 17(7), 866-880.

Stewart, G.R., Larher, F., Ahmad, I., and Lee, J.A. (1979). Nitrogen metabolism and salt tolerance in higher plant halophytes. In Ecological Processes in Coastal Environments (pp. 211-227). Oxford Blackwell.

Stuessy, T.F. (2007). Evolution of specific and genetic diversity during ontogeny of island floras: the importance of understanding process for interpreting island biogeographic patterns. In Biogeography in a Changing World (pp. 117-133). CRC Press.

USGS Products. (2014). Landsat 7 ETM+ SLC-off. US Department of the Interior, USGS EROS Center, https://earthexplorer.usgs.gov/.

USGS Products. (2016). Landsat 8 OLI/TIRS. US Department of the Interior, USGS EROS Center, https://earthexplorer.usgs.gov/.

Valente, L.M., Etienne, R.S., and Phillimore, A.B. (2014). The effects of island ontogeny on species diversity and phylogeny. Proceedings of the Royal Society B, 281, 20133227.

Vogel, S. (1984). Drag and flexibility in sessile organisms. American Zoologist, 24(1), 37-44.

Vorhaben, J.E., Klotz, A.V., and Campbell, J.W. (1984). Activity and oxidative metabolism of the land snail Helix aspersa. Physiological zoology, 57(3), 357-365.

Whittaker, R.J., Triantis, K.A., and Ladle, R.J. (2008). A general dynamic theory of oceanic island biogeography. Journal of Biogeography, 35, 977-994.

Williams, S.E., Marsh, H., and Winter, J. (2002). Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. Ecology, 83(5), 1317-1329.

Wright, R., Garbeil, H., Baloga, S.M., and Mouginis-Mark, P.J. (2006). An assessment of shuttle radar topography mission digital elevation data for studies of volcano morphology. Remote Sensing of Environment, 105, 41-53.

Yu, F., Wang, T., Groen, T.A., Skidmore, A.K., Yang, X., Geng, Y., and Ma, K. (2015). Multi-scale comparison of topographic complexity indices in relation to plant species richness. Ecological Complexity, 22, 93-101.