FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

THE RELATIONSHIP OF HETEROPTERA SPECIES RICHNESS, ABUNDANCE, AND MORPHOLOGY TO ELEVATIONAL GRADIENTS AND LAND-USE REGIMES ON MT. KILIMANJARO

An Undergraduate Honors Thesis submitted in partial fulfillment of the requirements

for the degree of Bachelors of Science

in

BIOLOGICAL SCIENCES

WITH HONORS

by

Joseph Paul Tardanico

2015

To: Dr. Timothy Collins, Chairperson Department of Biological Sciences

This Undergraduate Honors Thesis in Biological Sciences, written by Joseph Paul Tardanico entitled "The Relationship of Species Richness, Abundance, and Morphology to Elevational Gradients and Land-Use Regimes on Mt. Kilimanjaro", is submitted to you in partial fulfillment of the requirements for Undergraduate Honors in Biological Sciences. The Biological Sciences Undergraduate Honors Committee and the candidate's research supervisor(s) have read this thesis. We recommend that it be approved.

Suzanne Koptur

Dr. Suzanne Koptur
Honors Research Supervisor

Dr. Walter M. Goldberg, Chairperson,
Undergraduate Honors Committee

Date of Honors Research Presentation: April 20, 2015.
This thesis by Joseph Paul Tardanico is approved.

Dr. Timothy Collins, Chairperson,
Department of Biological Sciences

TABLE OF CONTENTS

CHAPTER PAGE

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

ACKNOWLEDGMENTS

I would like to thank the Deutscher Akademischer Austausch Dienst (DAAD, German Academic Exchange Service) for granting me a scholarship that allowed me to spend the 2013-2014 academic year conducting my honors thesis research in the Department of Animal Ecology & Tropical Biology (Zoology III) at the University of Würzburg. I would also like to thank Dr. Ingolf Steffan-Dewenter, the chair of Zoology III, for suggesting that I conduct my research in the lab of the Research Group Kilimanjaro, which he heads and which is funded by the Deutsche Forschungsgemeinschaft (DFG, the German Research Foundation). I additionally would like to thank the following persons: Dr. Marcell K. Peters, the scientific coordinator of the Research Group Kilimanjaro and the lab's postdoctoral researcher, who supervised my work at University of Würzburg and provided the R-software script that enabled me to begin my statistical analysis; my father, Dr. Richard Tardanico (Department of Global & Sociocultural Studies, Florida International University [FIU]), for his help in learning R and reviewing my thesis drafts; Dr. Walter Goldberg (Department of Biological Sciences, FIU) for setting high professional standards for the students in his Senior Honors Seminar during the spring of 2015 and for his detailed critiques of my many thesis drafts; and Dr. Mahadev Bhat (Department of Earth & Environment, FIU), under whom I have studied for an agroecology certificate at FIU, and whose program provided a U.S. Department of Agriculture grant that allowed me as a high school student to gain substantial research experience. Finally, I would like to thank Dr. Suzanne Koptur (Department of

Biological Sciences, FIU) for her generosity and patience in mentoring me as a budding ecologist since my high school years.

ABSTRACT OF THE THESIS

THE RELATIONSHIP OF HETEROPTERA SPECIES RICHNESS, ABUNDANCE, AND MORPHOLOGY TO ELEVATIONAL GRADIENTS AND LAND-USE REGIMES ON MT. KILIMANJARO

by

Joseph Paul Tardanico

Florida International University, 2015

Miami, Florida

Professor Suzanne Koptur, Major Professor

Insect biodiversity is unevenly distributed on local, regional, and global scales. Elevation is a key factor in the uneven distribution of insect diversity, serving as a proxy for a host of environmental variables. My study examines the relationship of Heteroptera (true bugs) species diversity, abundance, and morphology to elevational gradients and land-use regimes on Mt. Kilimanjaro, Tanzania, East Africa. Heteroptera specimens were collected from 60 research sites covering an elevational range of 3684m (866-4550m above sea level). Thirty of the sites were classified as natural, while the remaining 30 were classified as disturbed (e.g., agricultural use or converted to grasslands). I measured aspects of the body size of adult specimens and recorded their location of origin. I used regression models to analyze the relationships of Heteroptera species richness, abundance, and body measurements to elevation and land-use regime. Richness and abundance declined with greater elevation, controlling for land use. The declines were linear or logarithmic in form, depending on the model. Richness and abundance were greater in natural than disturbed sites, controlling for elevation. According to an interaction, richness decreased more in natural than disturbed sites with rising elevation. Body length increased as a quadratic function of elevation, adjusting for land use. Body width X length decreased as a logarithmic function of elevation, while leg length/body length decreased as a quadratic function. Leg length/body length was greater in disturbed than natural sites. Interactions indicated that body length and body width X length were greater in natural than disturbed sites as elevation rose, although the general trend was downward. Future research should examine the relative importance of land area, temperature, and resource constraints for Heteroptera diversity and morphology on Mt. Kilimanjaro.

INTRODUCTION

Insects are integral to biodiversity as pollinators, predators, and herbivores, but their biodiversity is unevenly distributed geographically around the world. Two key factors in their uneven distribution are latitude and elevation, both of which are proxies for variable geographic interactions between abiotic and biotic conditions. Associated with latitude is greater biodiversity in tropical than temperate zones (Gaston & Spicer 2004). However, the relationship of elevation to biodiversity is more complex, as research documents large variation in biodiversity along elevational gradients for different taxa (Gaston & Spicer 2004; Sundqvist et al. 2013). An increasingly important reason for such variation are patterns of habitat degradation caused by human activities (Schulze et al. 2004; Morris 2010). My study addresses three basic components of insect biodiversity—species richness, abundance, and morphology—in relation to elevational gradients and land-use regimes in a tropical montane ecosystem. The study specifically examines Heteroptera (the group of insects known as true bugs) on Mt. Kilimanjaro (Tanzania, East Africa). Heteroptera are pertinent to research on biodiversity as a large and diverse taxon that is ecologically and economically important, including as pests and as biological controls (Schuh and Slater 1995; Schaeffer and Panizzi 2000).

Drivers of insect diversity along elevational gradients

The elevational distribution of insect species reflects the interplay between their environmental tolerances and their interactions with other organisms. Elevation’s principal abiotic drivers of insect species distribution are land area and climate (Hansen & Rotella 1999; Hodkinson 2005; Körner 2007; Field et al. 2009;

Sundqvist 2013). Land area decreases as elevation rises, thereby restricting the space available for life (Lomolino 2001; Körner 2007). The main climatic factors associated with elevation and biodiversity are atmospheric pressure, temperature, and radiation (Körner 2007). Atmospheric pressure decreases by 11% with every kilometer increase in elevation. Temperature decreases on average by 0.6° Celsius per 100m of elevation. Solar radiation is greater, and partial pressures of oxygen and CO_2 are lower, at higher elevations (Barry 2008). Other climatic factors not directly related to elevation are precipitation, wind velocity, and seasonality (Körner 2007; Barry 2008).

Temperature directly affects rates of plant photosynthesis and metabolism and is therefore a controlling factor of primary production at varying elevations. Temperature also affects nutrient availability by controlling rates of mineralization (Sundqvist et al. 2013). Water availability likewise plays a critical role in determining plant community responses along elevation gradients (Sundqvist et al. 2013). Together, temperature and water availability influence the composition and structure of vegetation and thus the distribution of insect species (Hansen & Rotella 1999; Hodkinson 2005; Körner 2007; Sundqvist et al. 2013).

Through their effects on vegetation composition and structure, the abiotic variables influence rates of net primary productivity, which impose limits on productivity at higher trophic levels (Hansen & Rotella 1999; Sundqvist et al. 2013). Research suggests that higher rates of net primary productivity are associated with greater species abundance and richness (Hansen & Rotella 1999; Hodkinson 2005; Costanza et al. 2006). This relationship may be mediated, however, by locational variation in factors such as the trophic structure of communities (Peters et al. 2014), the effects of temperature on the foraging activities of ectothermic organisms (Classen et al. 2015), the strength of plant defense mechanisms (Pellisier et al. 2012), and the phenological impacts of climate change on insect-plant interactions (Benadi et al. 2014). Further, the relationship may be curvilinear, as rising species richness and abundance may flatten or turn downward after primary productivity reaches mid to high levels (Colwell et al. 2004). Such qualifications aside, vegetation composition and structure interact with local topography to influence environmental heterogeneity and thus shape patterns of insect species distribution along elevation gradients (Hansen & Rotella 1999; Bennett 2010). At any given location, the interactions are embedded within local histories of community assembly as well as wider landscape and regional ecological conditions (Hodkinson 2005; Field et al. 2009; Morris 2010; Tscharntke et al. 2012).

Insect species diversity in relation to elevational gradients and land-use regimes

A. Species richness and abundance

Species diversity for organisms in general varies considerably along elevation gradients depending on taxa and location. The two most commonly observed trends are a decline in diversity with increasing elevation or a mid-elevation peak (Hodkinson 2005; Rahbeck 2005; Sundqvist et al. 2013). Regarding insects, Leingärtner et al. (2014) documented a monotonic decline in species richness with increasing elevation for butterflies in the German Alps, a pattern which Larsen et al. (2011) reported for dung beetles in some Andean sites, Carneiro et al. (2013) for bees in the Brazilian Atlantic, and Classen et al. (2015) for bees on Mt. Kilimanjaro. Sanders (2002) observed mid-elevation peaks for ants at three sites in the western

United States, as did Brehm et al. (2007) for moths along the Barva Transect in Costa Rica and Despland et al. (2012) for butterflies in the Chilean Andes. Studies have occasionally reported that insect richness and abundance remain constant or even increase with rising elevation (Lawton et al. 1987; Romero and Avila 2001; Brehm and Fiedler 2004).

Declines in species diversity at high elevations are most basically associated with increased environmental stress, decreased available energy, and smaller habitat area (Lomolino 2001; McCain and Grytes 2010). The conditions underlying-mid elevation peaks in diversity are less well understood (Colwell et al. 2004). One explanation for such peaks regards elevation as a surrogate for primary productivity, and proposes that diversity increases curvilinearly with greater primary productivity (Sanders 2002). That is, diversity may initially rise with greater productivity, then peak at mid-level productivity and drop off at higher levels. There is little empirical evidence, however, that elevation is a valid surrogate for primary productivity (Rahbek 1995). An alternative explanation is that mid-elevation peaks result from overlapping ranges due to geometric constraints, which is called the mid-domain effect (Colwell and Lees 2002).

Some observed patterns of diversity may be artifacts of specific research methodologies (Lomolino 2001). Sampling regime and decreasing area with greater elevation may bias the results of studies. Terborgh (1977), Rahbek (1995), and Nogues-Bravo et al. (2008) found that the relationship of species richness to elevation changes from a monotonic decline with increasing elevation to a hump shaped relationship after controlling for sampling regime and land area. Incomplete or unequal sampling of elevation gradients may also bias results, as may latitudinal and seasonal influences (McCoy 1990; Lomolino 2001; Nogues-Bravo et al. 2008). However, insects and other organisms in tropical areas may have narrower physiological tolerances and thus narrower elevational ranges than their counterparts in temperate areas (Larsen et al. 2011).

Concerning land-use regimes, anthropogenic modifications exert a generally negative impact on biodiversity (Schulze et al. 2004; Morris 2010; Tscharntke et al. 2010, 2012). Modifications such as the clearance and use of land for charcoal, agriculture, roads, or towns eliminate, fragment, and in other ways degrade habitats. Such land-use changes create habitats that may be too small or otherwise too degraded for the survival of some species, and too disconnected to permit travel to suitable habitat fragments by less mobile species (Morris 2010; Tscharntke et al. 2010). The consequent loss of biodiversity, however, is frequently not linear. Different taxa respond in diverse and often variable ways to land-use changes, and both the spatial and temporal dimensions of biodiversity decline may be nonlinear (Schulze et al. 2004; Morris 2010; Kambach et al. 2013). Indeed, there may be substantial time delays in the loss of biodiversity, even if a particular habitat does not undergo further degradation (Krauss et al. 2010). Krauss et al. (2010) found that past landscapes are the best predictors of current habitat-specialized plant species richness in European grassland patches. Butterfly richness, however, was best predicted by current landscape area, demonstrating that short-lived organisms tend to respond much more quickly to habitat loss than do long-lived organisms.

B. Insect morphology

Research documents variation in adult insect body size with elevation, and suggests that such variation is adaptive (Hodkinson 2005; Dillon et al. 2006; Teuscher et al. 2009; Gaston & Chown 2013). For example, insect body size is related to basic morphological and physiological characteristics, and thus to adaptive capacities such as resistance to starvation and dessication, mating and fecundity, transport capacities and costs, and predation intensity (Gaston & Chown 2013). The subject of body size, then, is integral to insect biodiversity. The patterns of body-size variation, however, are diverse and their underlying mechanisms are unclear. Some insects display linear or curvilinear increases in adult size with greater elevation, while others display linear or curvilinear decreases or display no clear pattern at all. Given this wide variety of patterns, there are few empirical or theoretical generalities concerning adult insect size and elevation (Dillon et al. 2006; Teuscher et al. 2009; Chown & Gaston 2010; Shelomi 2012; Gaston & Chown 2013).

The principal factors affecting the relationship of adult insect body size to elevation are temperature, seasonality, and resource availability (Hodkinson 2005; Dillon et al. 2006; Chown & Gaston 2010). Increased size is commonly attributed to a negative association between developmental temperature and morphological size where resources are not a limiting factor. Decreased size, on the other hand, is commonly attributed to seasonal resource limitations (Hodkinson 2005). Nevertheless, the ability to generalize from these explanations is quite limited, as the size-altitude relationships of many insect species contradict predictions based on these patterns (Hodkinson 2005; Dillon et al. 2006; Chown & Gaston 2010; Shelomi

2012). Research within a related area of insect morphology hypothesizes that inconsistent taxa findings for leg length/body length ratio stem from a focus on habitat rugosity to the neglect of other possible factors such as variations in diet, foraging behavior, resource constraints, and social behavior (Chown and Parr 2004; Teuscher et al. 2009). To my knowledge, studies have not yet addressed insect leg length/body length ratio from the standpoint of elevation.

Inconsistent findings likewise characterize the sparse research literature on anthropogenic land-use change and insect body size. For example, Kambach et al. (2013) reported that the average body size of bees increases, but that of butterflies and moths decreases, in forest sites of human-induced fire damage compared with adjacent and other neighboring forest sites in the Bolivian Andes. Sukhodolskaya (2014) documented a complexity of relationships between the body sizes of ground beetles (*P.melanarius*) and conditions of anthropogenic land disturbance in Russia. My literature search did not identify any studies on the relationship of insect leg length/body length to land-use patterns.

Research questions

My study examines the following questions concerning the relationships of Heteroptera species diversity and adult body measurements (length, width X length, and leg length/body length) to elevational gradients and land-use regimes:

(1) Are the associations of Heteroptera species richness, abundance, and body measurements with elevational gradients positive or negative?

    a. Are the associations linear or non-linear (such as quadratic or logarithmic)?

(2) Are the associations of Heteroptera species richness, abundance, and body measurements with natural (versus disturbed) land-use sites positive or negative?

    a. Is there an interaction between land-use sites and elevation, such that richness, abundance, and body measurements increase or decrease in natural versus disturbed sites as elevation rises?

MATERIALS AND METHODS

Data collection

In this study I worked with Heteroptera specimens collected by S.W. Ferger of the DFG Research Group Kilimanjaro, headed by Dr. Ingolf Steffan-Dewenter (Department of Animal Ecology & Tropical Biology, University of Würzburg). Data collection was carried out using sweep nets at 60 different sites of 0.25 hectares on the southeast slopes of Mt. Kilimanjaro (2°45′-3°25′ S, 37°00′-37°43′). The sites were equally distributed across an elevation range from 866m to 4550m above sea level. The sampling was conducted between March 2011 and October 2012, once during the warm dry season (December to March) and once during the cold dry season (July to October). At each site specimens were collected along two parallel transects of 50m by sweep netting. The transects were slowly walked, for a total of 100 sweeps with a 30-cm diameter sweep net per site and study period. Two x study periods x 100 sweeps = 200 sweeps per study site were conducted.

Thirty of the 60 sampling sites are classified as natural. The other 30 are classified as disturbed, due to human interventions in the forms of home gardens, maize fields, coffee plantations, grasslands, selectively logged *Ocotea* forests, and fire disturbed *Podocarpus* forests (Classen et al. 2015). Mt. Kilimanjaro's base (700-1100m) is dominated by savanna vegetation. From 1100m to 1800m the vegetation becomes submontane and lower montane forests. It subsequently transitions to *Ocotea* forest (1800-2800m), *Podocarpus* forest (2800-3200m), *Erica* forest (3200-4000m), and alpine *Helichrysum* shrub (4000-4600m). Large areas of savanna and submontane forest have been cleared for agricultural use. Maize plantations are common in areas that used to be savanna or agroforestry systems. Many areas that once were submontane forest are now grasslands or have been converted into coffee plantations (Peters et al. 2014; Classen et al. 2015).

Half of the 60 sites yielded one or more Heteroptera specimens. Twenty-one (70%) of the natural sites and 9 (30%) of the disturbed sites yielded at least one specimen. Specimens from disturbed sites were mainly located at lower elevations, where the human land-use interventions occur. These specimens have a 32% shorter elevational range (866-3060m, range=2193m) compared to those from natural sites (960-4190m, range=3230m).

Members of the DFG Research Group Kilimanjaro placed the specimens in killing jars and then placed the specimens in vials filled with 70% ethanol to preserve them for later analysis. In the project's lab at the University of Würzburg, I measured small adult specimens using the reticle of a dissecting microscope (length (mm) = ocular units/magnification) or a ruler for specimens that were too large to measure with the microscope reticle. I measured length to the nearest 0.1mm from the tip of the head to the tip of the abdomen, and width at the widest point of the body. I measured leg length for the hind tibia only. As the final step, I recorded each measurement and the site where the specimen was collected.

There are differences in the number of observations between data sets. The richness-abundance data refer to number of sampling sites, whereas the observations of body measurements refer to number of specimens sampled. In addition, body measurements could not be made on damaged specimens, which thereby resulted in a narrower elevational range compared to that of richness-abundance.

Statistical methodology

I used R statistical software (version 3.1.2 for Windows) to analyze the data. In view of the pronounced right skewness of the count variables species richness and species abundance, I analyzed their relationships to elevation and land use by estimating two types of Generalized Linear Models (GLMs) for each dependent variable, as alternatives to OLS models. The GLM types are negative-binomial models (R {MASS} glm.nb) and Gamma models with log link (R {stats} glm). Negative-binomial models are appropriate for count dependent variables, but tend to perform most reliably with large sample sizes (Cameron and Trivedi 2013). Gamma models with log link are appropriate for highly right skewed quantitative dependent variables whose variance increases with larger values, and can accommodate smaller sample sizes (Cameron and Trivedi 2013). While negative-binomial models may represent the best functional fit for the study's count dependent variables, the relatively small sample size (*n* = 60) for species richness and species abundance casts doubt on the precision of the estimates (Cameron and Trivedi 2013). Thus I estimated Gamma models with a log link for comparison with the negative-binomial models. Given questions about which type of model is most appropriate to analyze species richness and species abundance, I estimated robust standard errors, which provide the most conservative estimates of standard errors and statistical significance (Cameron and Trivedi 2013). Both the negative-binomial and Gamma models yielded results that were more conservative (i.e. less likely to be statistically significant) than exploratory OLS models with a log transformation of the dependent variable. By this criterion the negative-binomial and Gamma models were preferable to the OLS models. The diagnostics for the negative-binomial and Gamma models also displayed more satisfactory model fit than the diagnostics for the OLS models.

Gamma models with robust standard errors are additionally appropriate for estimating the relationships of the body measurements to elevation and land use. I estimated the Gamma models (R {stats} glm) with a log link due to the right-skewed dependent variables.

For each of the study's dependent variables I estimated a series of models, some of which are nested. The first model of each series examines the dependent variable's linear relationship to elevation, without adjusting for land use. The second model includes elevation and the binary categorical variable natural versus disturbed land use. The third model addresses possible curvilinearity by including elevation as a logarithmic function, together with land use. The fourth model addresses another form of possible curvilinearity by expressing elevation as a quadratic function, while continuing to include land use. The fifth, and final, model tests for a possible interaction effect of elevation with land use on the dependent variable. The model diagnostics include Akaike Information Criterion (AIC) scores as an indicator of comparative model fit within a series of models that need not be nested. The lower the AIC score, the more comparatively plausible a model is within a series (Burnham and Anderson 2002)

The models do not include other predictors pertinent to elevational relationships such as land area, temperature, precipitation, and vegetation. These are potentially lurking variables that must be considered in the interpretation of the statistical results (Hansen & Rotella 1999; Peters et al. 2014; Classen et al. 2015;

Leingartner et al. 2015). Another possible limitation is that the elevational range of disturbed sites is roughly one-third narrower than that of natural sites, although each land-use category includes 30 sampling sites. The diagnostics for the body-measurement models were generally acceptable, including that there were no statistically influential outliers. The diagnostics suggest, however, that signs of non-constant variance, particularly for most of the leg length/body length models, might be reduced if the potentially lurking variables could be incorporated into the models.

RESULTS

The association between Heteroptera species richness and abundance is linear and strongly positive (r = .94, 95% CI [0.90, 0.96], P < .001; Table 1). The bivariate associations of both richness and abundance with elevation are negative and either approximately linear or slightly concave curvilinear, but are not statistically significant (Fig. 1a, 1b; Table 1). Richness and abundance are greater on average, at statistical significance, in natural than disturbed sites (Fig. 2a, 2b).

Table 1. Descriptive statistics of Mt. Kilimanjaro elevation (m), Heteroptera species richness, and Heteroptera species abundance for all sampling sites. N=number of sampling sites; range indicated by minimum and maximum (Min and Max).

	N	Mean	St. Dev.	Min	Max
elevation (m)	60	2,215.88	1,044.18	866	4,550
species richness	60	1.50	2.11	0	8
species abundance	60	2.53	3.78	0	16

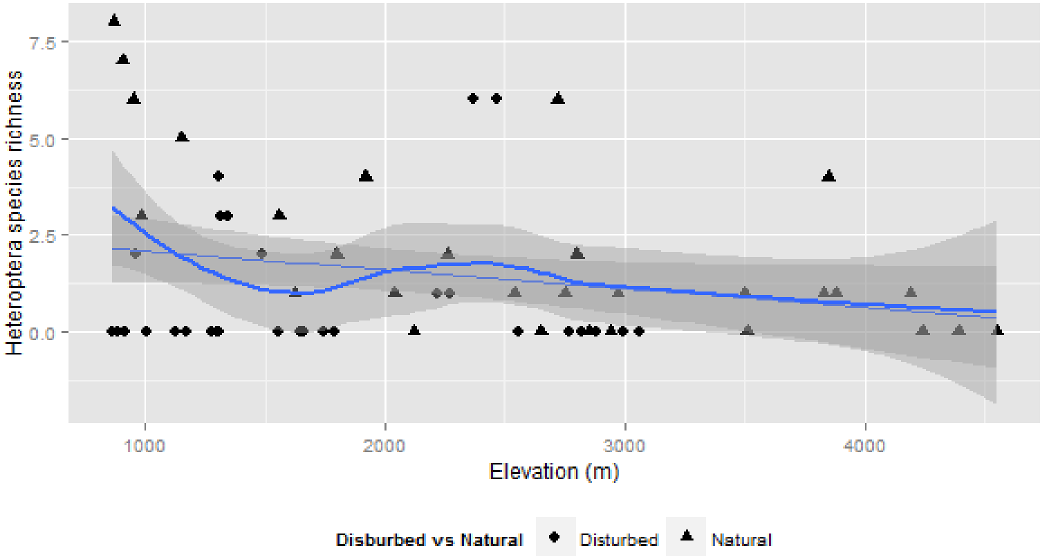

Figure 1a. The linear and loess smoother relationships of Mt. Kilimanjaro Heteroptera species richness to elevation (m) with 95% confidence intervals. Symbols indicate sampling sites and their land-use types: diamond = disturbed site (*n* = 30), triangle = natural natural site (*n* = 30). The Y-axis indicates the amount of species richness per site (0-8). The linear relationship represents a non-statistically significant negative association between species richness and elevation (*r* = -.239, 95% CI [-0.47, 0.02], *P* = .066). The possible curvilinear relationship indicated by the loess smoother is also a non-statistically significant negative association (Kendall rank tau = -0.133, z = -1.36, *P* = .173).

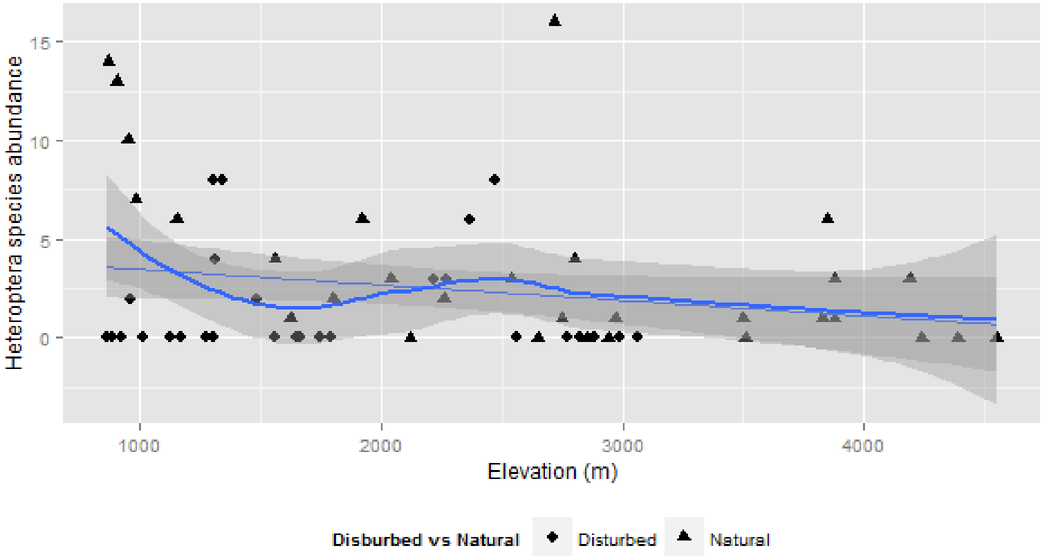

Figure 1b. The linear and loess smoother relationships of Mt. Kilimanjaro Heteroptera species abundance to elevation (m) with 95% confidence intervals. Symbols indicate sampling sites and their land-use types: diamond = disturbed site (*n* = 30), triangle = natural site (*n* = 30). The Y-axis indicates the amount of species abundance per site (0-16). The linear relationship represents a non-statistically significant negative association between species abundance and elevation (*r* = -.217, 95% CI [-0.45, 0.04], *P* = .096). The possible curvilinear relationship displayed by the loess smoother is also a non-statistically significant association (Kendall rank tau = -0.11, z = -1.14, *P* = .254).

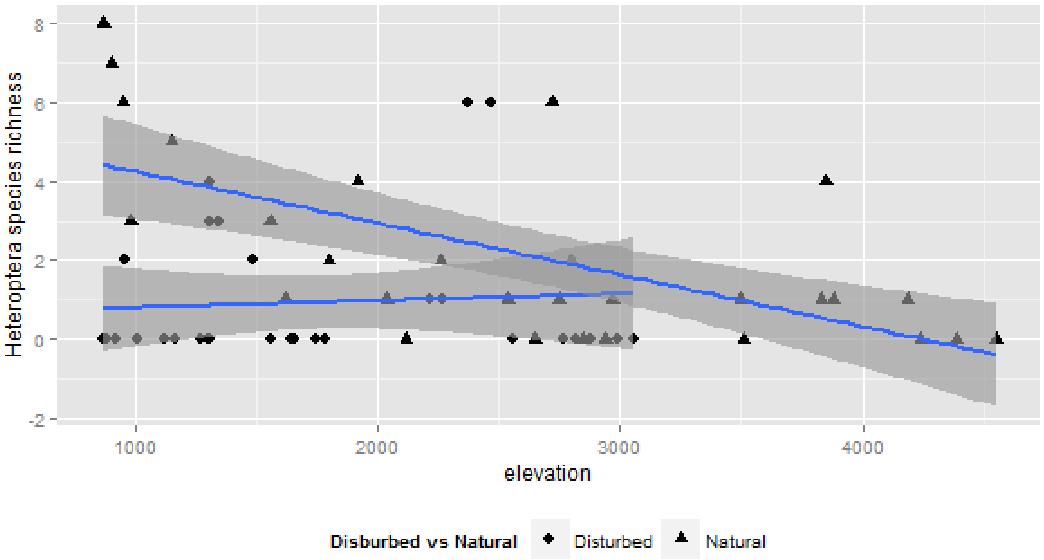

Figure 2a. The linear relationships of Mt. Kilimanjaro Heteroptera species richness to elevation (m) and land use with 95% confidence intervals. Symbols indicate sampling sites and their land-use types: diamond = disturbed site (*n* = 30), triangle = natural site (*n* = 30). The Y-axis indicates the amount of species richness per sampling site (0-8). Scatterplot lines also indicate types of land use: starting at lowest elevation, upper = natural sites, lower = disturbed sites. There is significantly more richness in natural than disturbed sites. Two-sample t-test: mean richess in natural sites = 2.07; mean richness in disturbed sites = 0.93; 95% CI [-2.194, -0.072]; t = -2.14, df = 54.3, *P* = .037. The descriptive relationship of richness to elevation is approximately constant for disturbed sites but negative for natural sites.

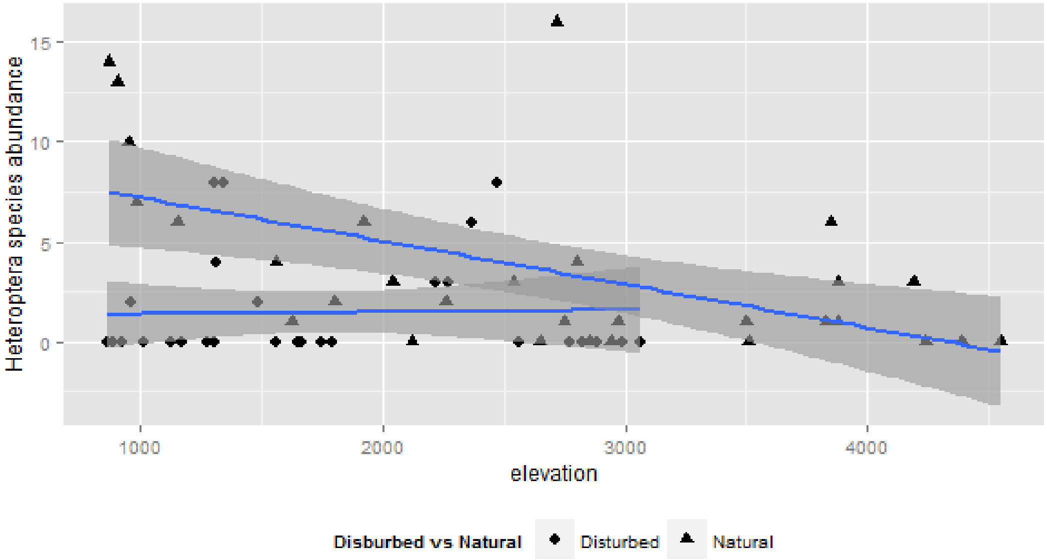

Figure 2b. The linear relationships of Mt. Kilimanjaro Heteroptera species abundance to elevation (m) and land use with 95% confidence intervals. Symbols indicate sampling sites and their land-use types: diamond = disturbed site (*n* = 30), triangle = natural site (*n* = 30). Scatterplot lines also indicate types of land use: starting at lowest elevation, upper = natural sites, lower = disturbed sites. The Y-axis indicates the amount of species abundance per sampling site (0-16). There is significantly more abundance in natural than disturbed sites. Two-sample t-test: mean abundance in natural sites = 3.60; mean abundance in disturbed sites = 1.47; 95% CI [-4.034, -0.233]; t = -2.26, df = 47.5, *P* = .029. The descriptive relationship of abundance to elevation is approximately constant for disturbed sites but negative for natural sites.

The regression models for adult body measurements examine body length, body width X length, and leg length/body length (Table 2). The bivariate associations of body length and body width X length with elevation are significantly negative and either are approximately linear or are concave curvilinear to varying degrees (Fig. 3a, 3b; Table 2). The bivariate association of leg length/body length with elevation is different from that of the other body measurements. Its linear relationship with elevation is positive but is not statistically significant, while its convex curvilinear relationship is positive and significant (Fig. 3c; Table 2).

Table 2. Descriptive statistics of Mt. Kilimanjaro elevation (m) and Heteroptera adult body measurements (mm) for undamaged specimens sampled. The number of observations differs from that reported for the data on Heteroptera species richness and abundance because the number of observations in the latter data refers to the number of sampling sites (*n* = 60) rather than to number of adult Heteroptera undamaged specimens as indicated in this table. The number of observations varies due to damaged specimens for which specific body measurements could not be made. The elevation range differs from that of the data for richness and abundance because these body measurement data exclude sampling sites at which no specimens were collected.

	N	Mean	St. Dev.	Min	Max
elevation (m)	152	1,883.00	955.00	871	4,190
body length (mm)	143	5.25	3.67	1.95	19.00
body width (mm)	145	1.72	0.74	0.80	6.42
leg length (mm)	123	3.12	2.35	0.20	10.90
body width X body length (mm^2)	143	9.90	9.92	1.66	73.80
leg length (mm)/body length (mm)	121	0.57	0.22	0.07	1.09

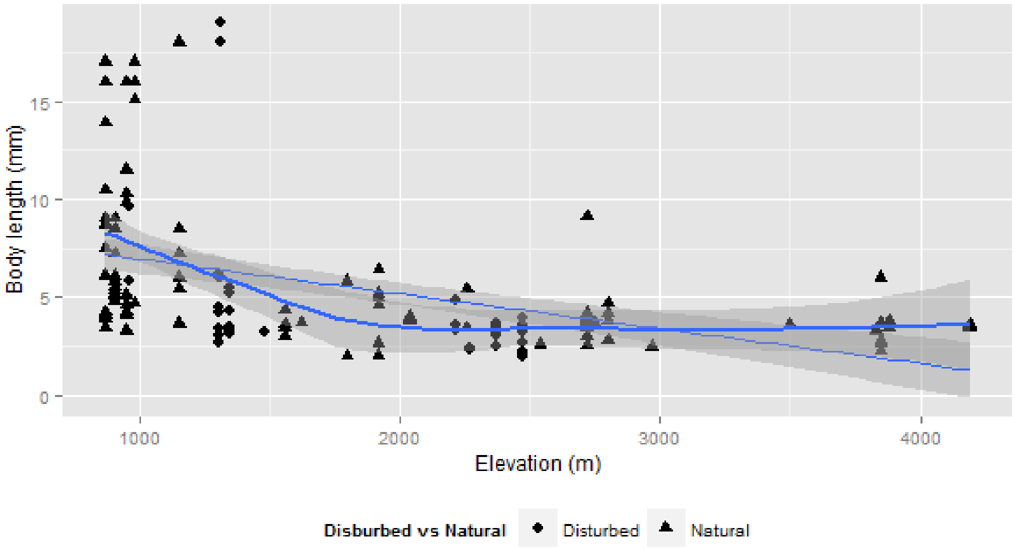

Figure 3a. The linear and loess smoother relationships of Mt. Kilimanjaro adult Heteroptera body length (mm) to elevation (m) with 95% confidence intervals. Symbols indicate sampling sites and their types of land use: diamond = disturbed site (*n* = 30), triangle = natural site (*n* = 30). The Y-axis indicates body length (mm) of sampled and undamaged adult specimens (*n* = 143). The linear relationship represents a statistically significant negative association between body length and elevation (*r* = -.459, 95% CI [-.581, -.316], *P* < .001). The possible curvilinear relationship indicated by the loess smoother also represents a statistically significant negative association (Kendall rank tau = -0.396, z = -6.72, *P* < .001).

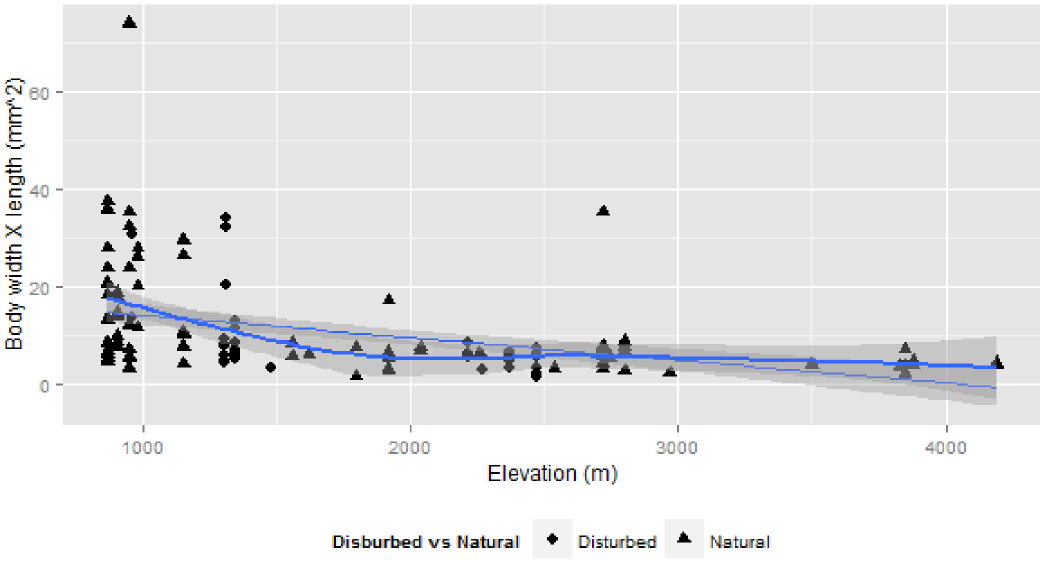

Figure 3b. The linear and loess smoother relationships of Mt. Kilimanjaro adult Heteroptera body width X length (mm2) to elevation (m) with 95% confidence intervals. Symbols indicate types of land use: diamond = disturbed sites, triangle = natural sites. The Y-axis indicates body width X length (mm^2) of sampled and undamaged adult specimens (*n* = 143). The linear relationship represents a statistically significant negative association between body width X length and elevation (*r* = -.441, 95% CI [-.566, -.296], *P* < .001). The possible curvilinear relationship indicated by the loess smoother also represents a statistically significant negative association (Kendall rank tau = -0.406, z = -6.92, *P* < .001).

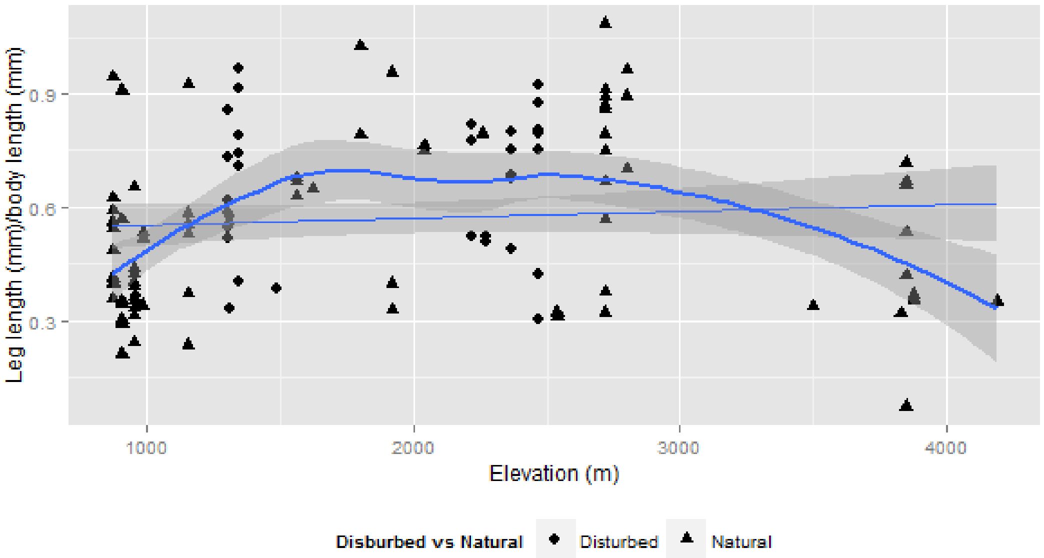

Figure 3c. The linear and loess smoother relationships of Mt. Kilimanjaro adult Heteroptera leg length (mm)/body length (mm) to elevation (m) with 95% confidence intervals (*n* = 121). Symbols indicate types of land use: diamond = disturbed site, triangle = natural sites. The Y-axis indicates the leg length (mm)/body length (mm) ratio of sampled and undamaged adult specimens (*n* = 121). The linear relationship represents a non-statistically significant positive association between leg length/body length and elevation (*r* = .080, 95% CI [-.102, .257], *P* = .387). The possible curvilinear relationship indicated by the loess smoother represents a statistically significant positive association (Kendall rank tau = 0.157, z = 2.46, *P* = .014).

Body length is significantly greater on average in natural than disturbed sites (Fig. 4a). The greater magnitude of body width X length in natural than disturbed sites is not statistically significant (Fig. 4b). Contrasting with the other body measurements, leg length/body length is significantly greater on average in disturbed than natural sites (Fig. 4c). In addition, leg length/body length is the only body measurement to display a descriptively positive relationship with elevation for disturbed sites (Fig. 4c).

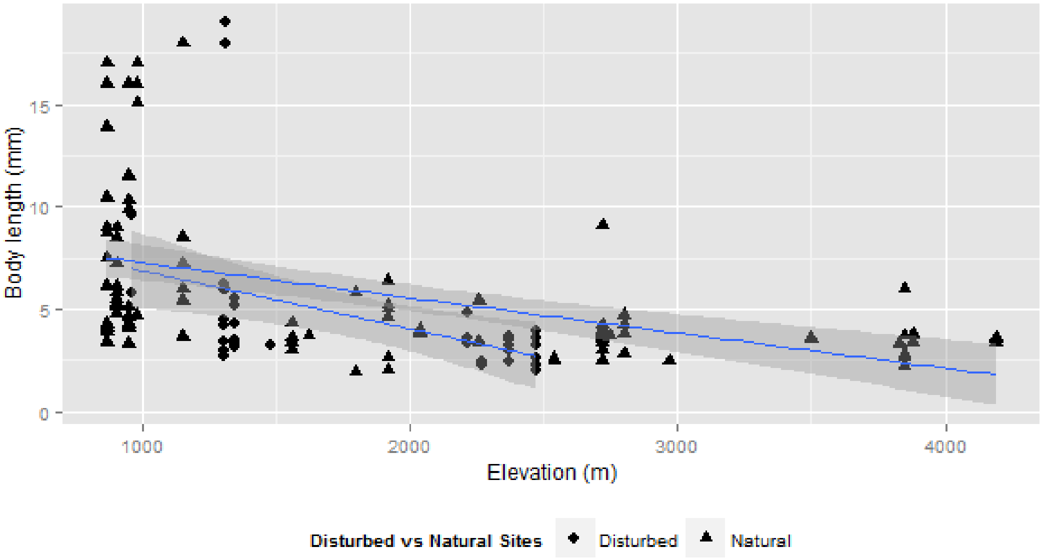

Figure 4a. The linear relationships of Mt. Kilimanjaro Heteroptera adult body length (mm) to elevation (m) and land use with 95% confidence intervals (*n* = 143). Symbols indicate types of land use: diamond = disturbed site, triangle = natural site. Scatterplot lines also indicate types of land use: starting at lowest elevation, upper = natural sites, lower = disturbed sites. Body length is not greater in natural than disturbed sites according to statistical significance in the parametric two-sample t-test (mean natural = 5.62mm, mean disturbed = 4.59mm; two-sample t-test (*t* = 1.52, df = 75, *P* = .134), but is significantly greater according to the non-parametric Wilcoxon-Mann-Whitney U-test (W = 1422, *P* = .010). The descriptive relationship of body length to elevation declines somewhat more steeply for disturbed than natural sites.

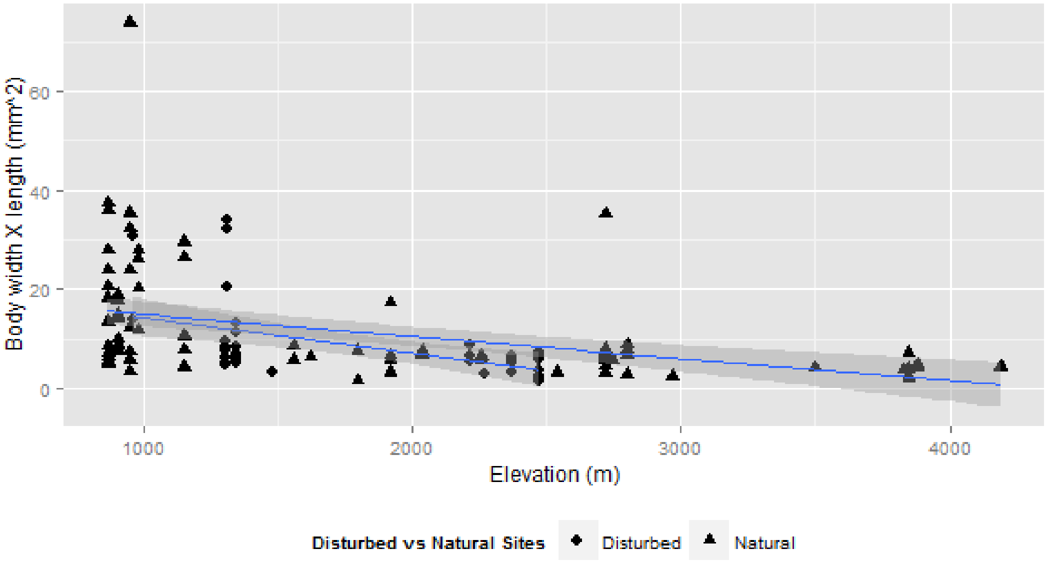

Figure 4b. The linear relationships of Mt. Kilimanjaro Heteroptera adult body width X body length (mm2) to elevation (m) and land use with 95% confidence intervals (*n* = 143). Symbols indicate types of land use: diamond = disturbed site, triangle = natural site. Scatterplot lines also indicate types of land use: starting at lowest elevation, upper = natural sites, lower = disturbed sites. Body width X length is descriptively greater in natural than disturbed sites, but this pattern is not statistically significant according to both the parametric t-test and the non-parametric Wilcoxon-Mann-Whitney U-test (mean natural = 10.70mm^2, mean disturbed = 8.55m^2; t = 1.32, df = 99.8, P = .189; W = 1756, P = .297). The descriptive relationship of body width X length to elevation declines somewhat more steeply for disturbed than natural sites.

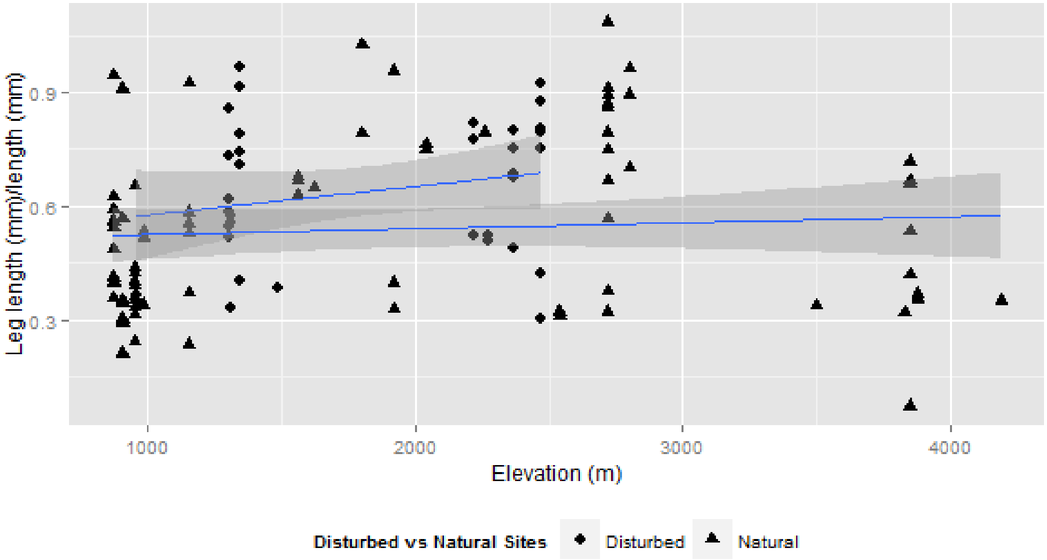

Figure 4c. The linear relationships of Mt. Kilimanjaro Heteroptera adult leg length (mm)/body length (mm) to elevation (m) and land use with 95% confidence intervals (*n* = 121). Symbols indicate types of land use: diamond = disturbed site, triangle = natural site. Scatterplot lines also indicate types of land use: starting at lowest elevation, upper = disturbed sites, lower = natural sites (which is different from the pattern displayed in the previous body measurement scatterplots). By contrast with the other body measurements, leg length/body length is significantly greater in disturbed than natural sites according to both the parametric two-sample t-test and the non-parametric Wilcoxon-Mann-Whitney U test (mean disturbed = 0.639, mean natural = 0.540; $t = 2.42$, df = 77.3, $P = .017$; W = 1860, $P = .017$). In further contrast with the other body measurements, the descriptive relationship of leg length/body length to elevation rises more steeply in disturbed than natural sites.

In summary, Heteroptera species richness and abundance display a strongly positive correlation with each other, but neither correlates with elevation at statistical significance. Both richness and abundance, however, are significantly greater on average in natural than disturbed sites. Body length and width X length display approximately linear or somewhat concave, significantly negative associations with elevation. Leg length/body length ratio deviates from the pattern of the other body measurements: its relationship with elevation is either approximately linear or convex, and is significantly positive. Body length is significantly greater on average in natural than disturbed sites, while body width X length is no different in natural than disturbed sites. Leg length/body length is significantly greater on average in disturbed than natural sites.

Turning to the regression models, elevation's relationship to Heteroptera species richness is negative in model 1's GLM Gamma and negative-binomial versions ($P < .05$), which do not adjust for land use (Tables 3 and 4). The relationship remains negative in both versions of model 2 ($P < .05$), which do adjust for land use. According to model 2, species richness is greater in natural than disturbed sites ($P <.05$). Models 3 and 4 explore different forms of possible curvilinearity in the relationship of Heteroptera species richness to elevation, holding land use constant (Tables 3 and 4). Elevation's logarithmic relationship to species richness is negative ($P < .05$) in the two variations of model 3. Species richness is greater in natural than disturbed sites ($P < .05$) according to the Gamma model, holding elevation constant, but the negative-binomial model's finding is not statistically significant. Elevation's quadratic relationship to species richness is not statistically significant in both types of model 4. The models continue to show, however, that species richness is significantly greater in natural than disturbed sites (Gamma, $P < .001$; negative-binomial, $P < .05$), holding elevation constant.

Table 3. Mt. Kilimanjaro Heteroptera species richness: GLM-Gamma models (log link) with robust standard errors. The column numbers refer to models. The Akaike Information Criterion (lowest score) indicates that model 5 is the most plausible model by a considerable margin: species richness declines more in natural than disturbed sites with rising elevation. This finding reflects the fact that species richness is greater in natural than disturbed sites at the lowest elevation sampled but then decreases as elevation increases, whereas species richness remains constant in disturbed sites as elevation increases (Fig. 2a).

	Heteroptera species richness				
	(1)	(2)	(3)	(4)	(5)
elevation (m)	-0.0002*	-0.0003**		0.0001	0.0001
	(0.0001)	(0.0001)		(0.001)	(0.0002)
log elevation (m)			-0.525*		
			(0.225)		
elevation (m)^{2}				-0.00000	
				(0.00000)	
natural vs disturbed sites		0.593*	0.532*	0.657**	1.580***
		(0.260)	(0.265)	(0.240)	(0.426)
elevation (m) X natural vs disturbed sites					-0.0005*
					(0.0002)
Constant	1.340***	1.180***	4.580**	0.770	0.474
	(0.242)	(0.191)	(1.580)	(0.501)	(0.368)
Observations	60	60	60	60	60
Log Likelihood	-107.000	-102.000	-103.000	-102.000	-99.100
Akaike Inf. Crit.	219.000	210.000	211.000	211.000	206.000

*p< .05; **p< .01; ***p< .001 (two-tailed)

Table 4. Mt. Kilimanjaro Heteroptera species richness: Negative-binomial models with robust standard errors. The column numbers refer to models. The Akaike Informational Criterion (lowest score) indicates that model 5 is the most plausible model in the series: species richness is greater on average in natural than disturbed sites, adjusting for elevation (Fig. 2a).

	Heteroptera species richness				
	(1)	(2)	(3)	(4)	(5)
elevation (m)	-0.0004*	-0.0005*		0.0003	0.0002
	(0.0002)	(0.0002)		(0.001)	(0.0004)
log elevation (m)			-0.849*		
			(0.394)		
elevation (m)^{2}				-0.00000	
				(0.00000)	
natural vs disturbed sites		0.994*	0.901	1.100*	2.600**
		(0.487)	(0.499)	(0.454)	(0.835)
elevation (m) X natural vs disturbed sites					-0.001
					(0.0005)
Constant	1.120**	0.762*	6.250*	-0.008	-0.452
	(0.392)	(0.341)	(2.690)	(0.882)	(0.771)
Observations	60	60	60	60	60
Log Likelihood	-99.100	-95.800	-96.300	-95.500	-94.200
theta	0.659** (0.224)	0.917* (0.373)	0.887* (0.357)	0.915* (0.364)	1.080* (0.477)
Akaike Inf. Crit.	202.000	198.000	199.000	199.000	196.000

*p< .05; **p< .01; ***p< .001 (two-tailed)

Model 5 tests for a possible interaction effect of elevation with land use. The interaction's coefficient is negative in the Gamma model (*P* < .05; Table 3). That is, according to this model, which the AIC scores indicate is the most plausible in the Gamma series, species richness decreases more in natural than disturbed sites as elevation increases. This finding reflects a downward slope in species richness for natural sites with rising elevation versus a constant relationship for disturbed sites (Fig. 1b). The negative-binomial version of model 5, which is the most plausible in its series, does not detect an interaction effect (Table 4). The model finds only that species richness is greater in natural than disturbed sites (*P* < .01), controlling for elevation.

To summarize, the best-fitting GLM Gamma model shows that elevation and land use negatively interact, with species richness decreasing in natural versus disturbed sites as elevation rises. This occurs as richness remains constant in disturbed sites, while sloping downward from a higher starting point for natural sites (Fig. 1b). The GLM negative-binomial models differ principally in not confirming an interaction between elevation and land use. Like the Gamma models, the negative-binomial models generally display greater richness on average in natural than disturbed sites and negative relationships of richness to elevation. Richness is descriptively greater in natural than disturbed sites until about 2250m, where the levels of richness converge (Fig. 1b).

Regarding Heteroptera species abundance, the Gamma and negative-binomial models display basically equivalent results (Tables 5 and 6). These results are similar to those of species richness with one notable difference: there is no significant interaction between elevation and land use for species abundance. The models with the lowest AIC scores (Gamma model 5, negative-binomial model 2) find that abundance is greater in natural than disturbed sites, correcting for elevation. The best-fitting negative-binomial model also documents a negative linear relationship of elevation with abundance, correcting for land use. As with richness, abundance is descriptively greater in natural than disturbed sites until approximately 2250m, where the levels equalize (Fig. 2b).

Table 5. Mt. Kilimanjaro Heteroptera species abundance: GLM-Gamma models (log link) with robust standard errors. The column numbers refer to models. The Akaike Information Criterion (lowest score) indicates that model 5 is the most plausible model in the series: species abundance is greater in natural than disturbed sites, adjusting for elevation. Model 2 is the second most plausible model: species abundance is greater on average in natural than disturbed sites, adjusting for elevation, while species abundance declines linearly with rising elevation, adjusting for land use (Fig. 2b).

	Heteroptera species abundance				
	(1)	(2)	(3)	(4)	(5)
elevation (m)	-0.0002	-0.0003^{**}		0.0002	0.0001
	(0.0001)	(0.0001)		(0.001)	(0.0003)
log elevation (m)			-0.618^{*}		
			(0.244)		
elevation $(m)^2$				-0.00000	
				(0.00000)	
natural vs disturbed sites		0.777^{**}	0.700^{*}	0.861^{**}	1.760^{**}
		(0.289)	(0.292)	(0.277)	(0.556)
elevation (m) X natural vs disturbed sites					-0.0005
					(0.0003)
Constant	1.740^{***}	1.510^{***}	5.510^{**}	0.997	0.807
	(0.298)	(0.247)	(1.760)	(0.627)	(0.484)
Observations	60	60	60	60	60
Log Likelihood	-134.000	-128.000	-129.000	-128.000	-126.000
Akaike Inf. Crit.	272.000	262.000	263.000	263.000	261.000

$^{*}p< .05$; $^{**}p< .01$; $^{***}p< .001$ (two-tailed)

Table 6. Mt. Kilimanjaro Heteroptera species abundance: Negative-binomial models with robust standard errors. The column numbers refer to models. The Akaike Information Criterion (lowest score) indicates that model 2 is the most plausible model in the series: species abundance is greater on average in natural than disturbed sites, adjusting for elevation, while species abundance declines linearly with rising elevation, adjusting for land use (Fig. 2b). Following closely behind model 2 are models 3 and 5. According to model 3, species abundance declines as a logarithmic function of elevation, adjusting for land use, while species abundance is greater on average in natural than disturbed sites, adjusting for log(elevation). According to model 5, species abundance is greater on average in natural than disturbed sites, adjusting for elevation.

	Heteroptera species abundance				
	(1)	(2)	(3)	(4)	(5)
elevation (m)	-0.0003	-0.0005**		0.0004	0.0001
	(0.0002)	(0.0002)		(0.001)	(0.0004)
log elevation (m)			-0.832*		
			(0.363)		
elevation (m)^{2}				-0.00000	
				(0.00000)	
natural vs disturbed sites		1.090*	0.978*	1.230**	2.410**
		(0.453)	(0.459)	(0.425)	(0.896)
elevation (m) X natural vs disturbed sites					-0.001
					(0.0004)
Constant	1.610***	1.220**	6.590*	0.307	0.210
	(0.406)	(0.374)	(2.560)	(0.940)	(0.824)
Observations	60	60	60	60	60
Log Likelihood	-120.000	-117.000	-117.000	-116.000	-116.000
theta	0.407***	0.500***	0.488***	0.507***	0.528***
	(0.111)	(0.148)	(0.144)	(0.150)	(0.160)
Akaike Inf. Crit.	243.000	239.000	240.000	241.000	240.000

*p<0.05; **p<0.01; ***p<0.001 (two-tailed)

In summary, the most general findings for Heteroptera species richness and abundance are that they are greater in natural than disturbed sites, holding elevation constant, and that they decline as a linear function of elevation, holding land use constant. A Gamma model, but not a negative-binomial model, detects a negative interaction of elevation and land use in regard to species richness, with richness declining in natural versus disturbed sites as elevation increases. This is due to a decreasing magnitude of species richness in natural sites with rising elevation, relative to an unchanging magnitude in disturbed sites. There is no such interaction for species abundance.

Only GLM Gamma models are estimated for adult Heteroptera body measurements. The relationship of Heteroptera body length to elevation is negative in model 1 ($P < .001$), which does not adjust for land use (Table 7). The negative relationship persists in model 2 ($P < .001$), which does adjust for land use. Body length is greater in natural than disturbed sites ($P < .05$), controlling for elevation. Models 3 and 4 address different forms of possible curvilinearity in body length's relationship to elevation. Elevation's logarithmic relationship to body length is negative in model 3 ($P < .001$), while its quadratic relationship to body length is positive in model 4 ($P < .001$), which according to the AIC scores is the most plausible model. Land use, which tests significant in model 2, becomes statistically non-significant in models 3 and 4. Model 5 detects a positive interaction between elevation and land use ($P < .05$). That is, with every meter increase in elevation, body length remains greater in natural than disturbed sites, even as body length trends downward in both land-use categories (Fig. 4a). This downward trend is less pronounced in natural than disturbed sites.

Table 7. Mt. Kilimanjaro Heteroptera adult body length: GLM Gamma models (log link) with robust standard errors. The column numbers refer to models. According to the Akaike Information Criterion (lowest score), model 4 is the most plausible model in the series: body length increases as a quadratic function of elevation, adjusting for land use (Figs. 3a, 4a).

	Heteroptera adult body length (mm)				
	(1)	(2)	(3)	(4)	(5)
elevation (m)	-0.0003***	-0.0003***		-0.001***	-0.001***
	(0.00005)	(0.00004)		(0.0002)	(0.0001)
log elevation (m)			-0.692***		
			(0.080)		
elevation (m)^2				0.00000***	
				(0.00000)	
natural vs disturbed sites		0.246*	0.176	0.126	-0.334
		(0.112)	(0.110)	(0.114)	(0.362)
elevation X natural vs disturbed sites					0.0003*
					(0.0002)
Constant	2.250***	2.090***	6.630***	2.830***	2.610***
	(0.117)	(0.148)	(0.634)	(0.248)	(0.342)
Observations	139	139	139	139	139
Log Likelihood	-304.000	-300.000	-295.000	-293.000	-297.000
Akaike Inf. Crit.	613.000	607.000	597.000	594.000	603.000

$^{*}p< .05$; $^{**}p< .01$; $^{***}p< .001$ (two-tailed)

Body width X length decreases as either a linear or logarithmic function of elevation in all of the models ($P < .001$), whether or not they control for land use (Table 8). The AIC scores point to model 3, in which width X length decreases as a logarithmic function of elevation, as the best-fitting model. According to model 2, body width X length is greater in natural than disturbed sites ($P < .05$), controlling for elevation, but land use becomes statistically non-significant in models 3 and 4. The interaction of land use with elevation tests positive in model 5 ($P < .05$). Thus, body width X length is greater in natural than disturbed sites as elevation rises. Body width X length appears to diminish incrementally in natural sites with rising elevation, while on average remaining greater than in disturbed sites, where it does not vary by elevation (Fig. 4b).

Table 8. Mt. Kilimanjaro Heteroptera adult body width X length (mm2): GLM Gamma models (log link) with robust standard errors. The column numbers refer to models. The Akaike Information Criterion (lowest score) indicates that model 3 is the most plausible model in the series: body width X length decreases as a logarithmic function of elevation, adjusting for land use (Fig. 3b). The second most plausible model is model 5: body width X length is greater on average in natural than disturbed sites with rising elevation (Fig. 4b).

	Heteroptera adult body width X length (mm^2)				
	(1)	(2)	(3)	(4)	(5)
elevation	-0.0005***	-0.001***		-0.001**	-0.001***
	(0.0001)	(0.0001)		(0.0003)	(0.0002)
log elevation (m)			-0.991***		
			(0.124)		
elevation (m)^2				0.00000	
				(0.00000)	
natural vs disturbed sites		0.276*	0.179	0.195	-0.391
		(0.134)	(0.132)	(0.153)	(0.403)
elevation (m) X natural vs disturbed sites					0.0004*
					(0.0002)
Constant	3.140***	2.970***	9.430***	3.500***	3.570***
	(0.153)	(0.173)	(0.952)	(0.409)	(0.368)
Observations	139	139	139	139	139
Log Likelihood	-417.000	-414.000	-412.000	-412.000	-412.000
Akaike Inf. Crit.	838.000	835.000	830.000	833.000	832.000

$^{*}p< .05$; $^{**}p< .01$; $^{***}p< .001$ (two-tailed)

Leg length/body length ratio is the only body measurement to correlate positively with elevation and to be greater on average in disturbed than natural sites (Fig. 4c). Concerning the regression results, elevation's logarithmic relationship to leg length/body length is positive in model 3, adjusting for land use (Table 9). However, the AIC scores clearly support model 4, in which elevation's quadratic relationship to leg length/body length is negative (*P* < .001). Land use is significant only in model 2 (*P* < .01) and model 3 (*P* < .05), which correct for elevation as either a linear or logarithmic function. The coefficients for land use are negative, as, according to models 2 and 3, leg length/body length is greater in disturbed than natural sites. There is no interaction effect of land use and elevation for leg length/body length.

Table 9. Mt. Kilimanjaro adult Heteroptera leg length (mm)/body length (mm): GLM Gamma models (log link) with robust standard errors. The column numbers refer to models. The Akaike Information Criterion (lowest score) indicates that model 4 is the most plausible model in the series: length length/ body length ratio decreases as a quadratic function of elevation, adjusting for land use (Fig. 3c).

	Heteroptera leg length (mm)/body length (mm)				
	(1)	(2)	(3)	(4)	(5)
elevation (m)	0.00004	0.00004		0.001***	0.0001
	(0.00004)	(0.00004)		(0.0002)	(0.0001)
log elevation (m)			0.153*		
			(0.073)		
elevation (m)^{2}				-0.00000***	
				(0.00000)	
natural vs disturbed sites		-0.173*	-0.163*	-0.021	-0.012
		(0.067)	(0.067)	(0.071)	(0.203)
elevation (m) X natural vs disturbed sites					-0.0001
					(0.0001)
Constant	-0.637***	-0.529***	-1.590**	-1.470***	-0.672***
	(0.076)	(0.085)	(0.545)	(0.190)	(0.185)
Observations	118	118	118	118	118
Log Likelihood	10.800	13.200	14.600	26.100	13.400
Akaike Inf. Crit.	-17.700	-20.300	-23.200	-44.100	-18.800

*p<0.05; **p<0.01; ***p<0.001 (two-tailed)

Summing up, the most plausible model for body length finds that it increases as a quadratic function of elevation, controlling for land use. Body width X length decreases as a logarithmic function of elevation, while leg length/body length decreases as a quadratic function. Non-linear elevational relationships are the principal predictors of body measurements. As secondary findings, body length and width X length are greater in natural than disturbed sites with rising elevation, even as their trajectories are downward (Figs. 4a, 4b). Leg length/body length is greater in disturbed than natural sites (Fig. 4c).

DISCUSSION

This study examined Heteroptera species richness, abundance, and adult body measurements in relation to elevational gradients and land-use regimes on Mt. Kilimanjaro. Species richness and abundance did not correlate significantly with elevation. According to regression models, however, species richness and abundance decreased with rising elevation, controlling for land-use regime. This decrease was linear in the best-fitting models but was significantly logarithmic in another model. The linear finding is consistent with the temperature limitation and the metabolic theory of ecology, both of which predict a linear decline in richness due to decreasing temperature (Clarke and Gaston 2006; McCain 2007; Sanders et al. 2007). The logarithmic finding suggests that factors besides temperature influence Heteroptera richness and abundance patterns. The study did not directly examine the effects of climate, resource constraints, and land area on species richness and abundance. Controlling for these factors could potentially change the relationships of richness and abundance to elevation, as well as to land-use regimes.

Heteroptera species richness and abundance were significantly greater in natural sites than disturbed sites, whether or not controlling for elevation. By contrast, Classen et al. (2015) reported that land-use regimes on Mt. Kilimanjaro did not significantly affect bee species richness. They attributed the absence of this effect to the moderate degree of human land-use interventions on Mt. Kilimanjaro. The dominant agricultural system on Mt. Kilimanjaro is small-scale subsistence farming, which maintains high levels of semi-natural areas in and around crop fields. Peters et al. (2014), nonetheless, found that ant species richness on Mt. Kilimanjaro declines linearly with greater elevation for natural sites, while displaying a mid-elevation peak for disturbed sites. They concluded that this difference is due to resource constraints that vary with elevational changes in land use. My study's findings reinforce the literature on taxa-specific insect responses to both elevation and disturbance by human activity (Schulze et al. 2004; Hodkinson 2005; Morris 2010; Larsen et al. 2011; Tscharntke et al. 2012; Sundqvist et al. 2013).

My study additionally explored the interaction of elevation with land-use regimes in regard to species richness and abundance. The interaction tested significant only in one GLM-Gamma model for richness. In this case, richness declined in natural relative to disturbed sites with rising elevation. This is because species richness is comparatively low in disturbed sites, where the relationship between richness and elevation is constant. The finding of the interaction suggests that resource constraints in disturbed sites regardless of elevation, and in natural sites with rising elevation, may limit Heteroptera diversity on Mt. Kilimanjaro. Future research should examine the relative importance of temperature and resource constraints for Heteroptera on Mt. Kilimanjaro.

Bivariate associations displayed negative relationships of adult body length and body width X length with elevation, but found an increase for leg length/body length. The associations also confirmed that body length was greater in natural than disturbed sites, but found that body width X length did not vary between land-use types and that leg length/body length was greater in disturbed than natural sites. For the regression models, the AIC model-selection criterion principally indicated a quadratic increase in body length with rising elevation, adjusting for land use. There was a logarithmic decrease for body width X length, together with a quadratic decrease for leg length/body length. The AIC criterion secondarily indicated two positive interaction effects, as body length and width X length increased in natural versus disturbed sites with rising elevation. These positive interactions point toward the possibility of greater resource availability in natural than disturbed sites.

The results for body measurements should be interpreted within the literature's emphasis on taxa-specific associations of insect body measurements with elevation (Hodkinson 2005; Dillon et al. 2006; Chown and Gaston 2010; Gaston and Chown 2013) and with land use (Kambach et al. 2013; Sukhodolskaya 2014). That is, research does not find consistent taxa-specific patterns in this relationship. To my knowledge, my study's results represent a first step in exploring the relationship of insect leg length/body length to elevation as well as land-use regime (Chown and Parr 2004; Teuscher et al. 2009). Future studies on the relationship of body measurements to elevation and land-use regime on Mt. Kilimanjaro might examine the results comparatively by species. Studies might also explore the relationship by testing the hypotheses presented by Chown and Gaston (2010) and Gaston and Chown (2013), the most promising of which they regard as the combined resource allocation model.

LITERATURE CITED

Barry RG. 2008. Mountain weather and climate (3rd ed.). Cambridge, UK: Cambridge University Press.

Benadi G, Hovestadt T, Poethke H, Blüthgen N. 2014. Specialization and phenological synchrony of plant-pollinator interactions along an altitudinal gradient. Journal of Animal Ecology 83:639-650. doi:10.1111/1365-2656.12158

Bennett A. 2010. The role of soil community biodiversity in insect biodiversity. Insect Conservation and Diversity 3:157-171. doi:10.1111/j.1752-4598.2010.00086.x

Brehm G, Colwell RK, Kluge J. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. Global Ecology and Biogeography 16: 205-219. doi:10.1111/j.1466-8238.2006.00281.x

Brehm G, Fiedler K. 2004. Bergmann's rule does not apply to geometrid moths along an elevational gradient in an Andean montane rain forest. Global Ecology and Biogeography 13:7-14. doi:10.1111/j.1466-882X.2004.00069.x

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference (2nd ed.). New York: Springer.

Cameron AC, Trivedi PK. 2013. Regression analysis of count data (2nd ed.). Cambridge: Cambridge University Press.

Carneiro EM, Mielke OHH, Casagrande MM, Fielder K. 2014. Skipper richness (Hesperiidae) along elevational gradients in Brazilian Atlantic forest. Neotropical Entomology 43:27-38. doi: 10.1007/s13744-013-0175-8

Chown SL, Gaston KJ. 2010. Body size variation in insects: A macroecological perspective. Biological Reviews 85:139-169. doi:10.1111/j.1469-185X.2009.00097.x

Chown SL, Parr CL. 2004. RESPONSE - pattern, process, and the size-grain hypothesis. Ecological Entomology 29:381-382. doi:10.1111/j.1365-2311.2004.00606.x/epdf

Clarke A, Gaston KJ. 2006. Climate, energy and diversity. Proceedings of the Royal Society of London B: Biological Sciences 273:2257-2266. doi:10.1098/rspb.2006.3545

Classen A, Peters MK, Kindeketa WJ, et al. 2015. Temperature versus resource constraints: Which factors determine bee diversity on Mount Kilimanjaro, Tanzania? Global Ecology and Biogeography n/a-n/a doi:10.1111/geb.12286

Colwell RK, Lees DC. 2002. The mid-domain effect: Geometric constraints on the geography of species richness. Trends in Ecology & Evolution 15:70-76. doi:10.1016/S0169-5347(99)01767-X

Costanza R, Fisher B, Mulder K, et al. 2007. Biodiversity and ecosystem services: A multi-scale empirical study of the relationship between species richness and net primary production. Ecological Economics 61:478-491. doi:10.1016/j.ecolecon.2006.03.021

Despland E, Humire R, San Martin S. 2012. Species richness and phenology of butterflies along an altitude gradient in the desert of northern Chile. Arctic, Antarctic, and Alpine Research 44:423-431. doi:10.1657/1938-4246-44.4.423

Dillon ME, Frazier MR, Dudley, R. 2006. Into thin air: Physiology and evolution of alpine insects. Integrative and Comparative Biology 46:49-61. doi:10.1093/icb/icj007

Field R, Hawkins BA, Cornell HV, et al. 2009. Spatial species-richness gradients across scales: A meta-analysis. Journal of Biogeography 36:132-147. doi:10.1111/j.1365-2699.2008.01963.x

Gaston KJ, Chown SL. 2013. Macroecological patterns in insect body size. In: Animal body size: Linking pattern and process across space, time, and taxonomic group, ed. Smith FA, Lyons SK, pp. 13-61. Chicago: University of Chicago Press. doi:10.7208/chicago/9780226012285.003.0002

Gaston KJ, Spicer JI. 2004. Biodiversity (3rd ed.). Oxford: Wiley-Blackwell.

Hansen AJ, Rotella JR. 1999. Abiotic factors in biodiversity. In: Maintaining biodiversity in forest ecosystems, ed. Hunter ML, pp. 161-209. Cambridge, UK: Cambridge University Press. doi:10.1017/CBO9780511613029

Hodkinson ID. 2005. Terrestrial insects along elevation gradients: Species and community responses to altitude. Biological Reviews 80:489-513. doi:10.1017/S1464793105006767

Kambach S, Guerra F, Beck SG, et al. 2013. Human-induced disturbance alters pollinator communities in tropical montane forests. Diversity 5:1-14. doi:10.3390/d5010001

Körner C. 2007. The use of 'altitude' in ecological research. Trends in Ecology & Evolution 22:569-574. doi:10.1016/j.tree.2007.09.006

Larsen TH, Escobar F, Armbrecht I. 2011. Insects of the tropical Andes: Diversity patterns, processes, and global change. In: Climate change and biodiversity in the tropical Andes, ed. Herzog SK, Martínez R, Jørgensen PM, Tiessen H, pp. 228-244. São José dos Campos, Brazil and Paris: Inter-American Institute of Global Change

Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE). http://goo.gl/gGlZRR

Lawton JH, MacGarvin M, Heads PA. 1987. Effects of altitude on the abundance and species richness of insect herbivores on bracken. Journal of Animal Ecology 56:147-160.

Leingärtner A, Krauss J, Steffan-Dewenter I. 2014. Species richness and trait composition of butterfly assemblages change along an altitudinal gradient. Oecologia 175:613-23. 0.1007/s00442-014-2917-7

Lomolino MV. 2001. Elevation gradients of species-density: Historical and prospective views. Global Ecology and Biogeography 10:3-13. 10.1046/j.1466-822x.2001.00229.x

McCain CM. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. Global Ecology and Biogeography 16:1-13. doi:10.1111/j.1466-8238.2006.00263.x

McCain CM, Grytnes J. 2010. Elevational gradients in species richness. In: eLS. John Wiley & Sons, Chichester. www.els.net [doi:10.1002/9780470015902.a0022548]

McCoy ED. 1990. The distribution of insects along elevational gradients. Oikos 58:313-322.

Morris R.J. 2010. Anthropogenic impacts on tropical forest biodiversity: A network structure and ecosystem functioning perspective. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:3709-3718. doi:10.1098/rstb.2010.0273

Nogues-Bravo D, Araujo MB, Romdal T, Rahbek C. 2008. Scale effects and human impact on the elevational species richness gradients. Nature 453:216-219. doi:10.1038/nature06812

Pellissier L, Fiedler K, Ndribe C, et al. 2012. Shifts in species richness, herbivore specialization, and plant resistance along elevation gradients. Ecology and Evolution 2:1818-1825. doi:10.1002/ece3.296

Peters MK, Mayr A, Röder J, et al. 2014. Variation in nutrient use in ant assemblages along an extensive elevational gradient on Mt. Kilimanjaro. Journal of Biogeography 41:2245-2255. doi:10.1111/jbi.12384

Rahbek C. 1995. The elevational gradient of species richness: A uniform pattern? Ecography 18:200-205. doi:10.1111/j.1600-0587.1995.tb00341.x

Rahbek C. 2005. The role of spatial scale and the perception of large-scale species–richness patterns. Ecology Letters 8:224-229. doi:10.1111/j.1461-0248.2004.00701.x

Romero AE, Avila JM. 2000. Effect of elevation and type of habitat on the abundance and diversity of scarabacoid dung beetle (Scarabaeoidea) assemblages in a Mediterranean area from southern Iberian Peninsula. Zoological Studies 39:352-359.

Sanders NJ. 2002. Elevational gradients in ant species richness: Area, geometry, and Rapoport's rule. Ecography 25:25-32. doi:10.1034/j.1600-0587.2002.250104.x

Sanders NJ, Lessard J, Fitzpatrick MC, Dunn RR. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16:640-649. doi:10.1111/j.1466-8238.2007.00316.x

Schaefer CW, Panizzi AR. (eds.). (2000). Heteroptera of economic importance. Boca Raton, FL: CRC Press.

Schuh RT, Slater JA (1995). True bugs of the world (Hemiptera Heteroptera). Ithaca: Cornell University Press.

Schulze CH, Waltert M, Kessler PJ, et al. 2004. Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. Ecological Applications 14:1321-1333. doi:10.1890/02-5409

Shelomi M. 2012. Where are we now? Bergmann's rule *sensu lato* in insects. The American Naturalist 180:511-519. doi:10.1086/667595

Sukhodolskaya R. 2014. Variation in body size and body shape in ground beetle *Pterostichus melanarius* (Coleoptera, Carabidae). Journal of Agri-Food and Applied Sciences 2:196-205. http://blue-ap.org/j/Journal_of_Agri-Food_and_Applied_Sciences/Issue-Volume%202%20%282014%29-Issue%2007

Sundqvist MK, Sanders NJ, Wardle DA. 2013. Community and ecosystem responses to elevational gradients: Processes, mechanisms, and insights for global change. Annual Review of Ecology, Evolution, and Systematics 44:261-280. doi:10.1146/annurev-ecolsys-110512-135750

Terborgh J. 1977. Bird species diversity on an Andean elevational gradient. Ecology, 58(5): 1007-1019.

Teuscher M, Brandle M, Traxel V, Brandle R. 2009. Allometry between leg and body length of insects: Lack of support for the size-grain hypothesis. Ecological Entomology 34:718-724. doi:10.1111/j.1365-2311.2009.01124.x

Tscharntke T, Leuschner C, Veldkamp E, et al. 2010. Tropical rainforests and agroforests under global change. Heidelberg, Germany: Springer.

Tscharntke T, Tylianakis JM, Rand TA, et al. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews 87:661-685. doi:10.1111/j.1469-185X.2011.00216.x