

ORIGINAL ARTICLE

Carabid beetle diversity and community composition as related to altitude and seasonality in Andean forests

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Carabid beetle (Coleoptera: Carabidae) diversity and community composition was investigated along an altitudinal gradient from 1400 m to 3400 m in southeastern Peru, utilizing recently published data of the first systematic inventory of carabid beetles in the region. The study transect is located in one of the highest biological diversity regions in the world. Active and passive collection techniques were used to examine temporal (rainy and dry seasons) and spatial (altitude) structure of adult carabid beetle assemblages. After adjusting for collection effort, species richness, as estimated by the Mao Tau richness estimator, peaked at 2000 m, some 600 meters above the lowest sampled altitude in this study. Similarity between species assemblages from different altitudinal sites was $\leq 52\%$. Species richness was approximately 10% higher in the rainy season than the dry season, with 64% of species occurring in both seasons. Despite the importance of multi seasonal survey sampling for Neotropical habitats, most surveys to date have been limited to the dry season. Studies of organisms that can serve as indicators of habitat shift along altitudinal gradients become increasingly relevant with predicted global climate change.

Se realizó la investigación de la diversidad y composición de comunidades de los escarabajos Carabidae (Coleóptero) en el sureste de Perú, investigando a lo largo de un gradiente altitudinal, de 1400 m a 3400 m, utilizando datos recién publicados del primer inventario sistemático de los escarabajos Carabidae de la región. El área de estudio se encuentra dentro de una de las regiones con más alta diversidad en el mundo. Se colectaron siguiendo metodologías activas y pasivas para examinar la estructura de las comunidades de carábidos en escalas temporales (temporadas de lluvia o seco) y espaciales (altura). Después de ajustar el número de especies, la riqueza de especies, estimado por riqueza de Mao Tau, fue más alta a los 2000 m, a unos 600 m sobre la altitud más bajo del muestreo de este estudio. La similitud entre el conjunto de especies en el gradiente altitudinal fue $\leq 52\%$. La riqueza de especies fue aproximadamente 10% más alta en la temporada de lluvias que en la de seca, con una similitud en la composición de las especies a casi 64% entre estaciones. A pesar de la importancia del muestreo multi estacional en los hábitat Neotropicales, la mayoría de los estudios han sido mono estacionales, y muchos de ellos se llevaron durante la estación seca. Con la alta probabilidad del cambio climático y las amenazas a la biodiversidad en todo el mundo, los estudios cuantitativos pueden servir como indicadores del cambio de hábitat a lo largo de gradientes altitudinales en ecosistemas tropicales.

Keywords: altitudinal gradient; Carabidae; mid domain effect; Puna; southeastern Peru; tropical rainforest

Introduction

Species diversity and community assemblages are often examined on naturally occurring environmental gradients such as altitudinal transects. Distribution of organisms along altitudinal gradients in tropical forests has been a long-standing question (e.g. von Humboldt & Bonpland 1807). Montane systems are an ideal setting to study species distributions because environmental factors often vary predictably with the altitudinal gradient (Lessard et al. 2010). Distinct communities of insects are found along an altitudinal gradient because, as ectotherms, insects are especially sensitive to temperature change (Deutsch et al. 2008). Altitudinal patterns of diversity have been well studied in insects groups such as Lepidoptera (Brehm

et al. 2003; Chen et al. 2009) and Coleoptera, including families Scarabaeidae (Hanski & Niemelä 1990; Escobar et al. 2005) and Carabidae (Darlington 1943; Hosoda 1999; Moret 2009). According to projected climate change models, many tropical montane ecosystems are likely to disappear as lowland habitats advance upslope (Williams et al. 2007). With recent estimates for terrestrial taxa suggesting that species distributions may increase in altitude at a rate of 11 m per decade (Chen et al. 2011), it is important to begin documentation of current species distribution and richness patterns as a point of reference for future studies.

Maveety et al. (2011) described the diversity of carabid beetles (Coleoptera: Carabidae) in the cloud

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forests of southeastern Peru (from approximately 1500 m to 3400 m) over a one-year period. Their results reported the first systematic collection of carabid beetles on an altitudinal gradient in the Neotropics. Collections included both active (hand searches) and passive (pitfall trap) collections and reported that active hand searches are the preferred method for carabid beetle collections in the tropics. Active collections yielded almost four times as many individuals as passive pitfall traps, and sampled approximately twice as many species; most species found in pitfall traps were also found in hand collections and the two techniques collected similar assemblages. Multiple collection techniques are often employed for total biodiversity surveys (e.g. see Erwin 1996), but hand collections have proved more efficient for ground surface collections of carabid beetles in the Neotropics (Maveety et al. 2011).

This study utilizes the same dataset of Maveety et al. (2011), but here examines species diversity and community structure through space (altitude) and time (seasonality). Various trends have been observed for diversity as it relates to altitude. Species richness declines monotonically with altitude, e.g. in Neotropical tree species (Gentry 1988), syntopic birds in Peru (Terborgh 1977), and raw species number of carabid beetles in Peru (Maveety et al. 2011), or there is a peak at the middle altitudes, e.g. small mammals in Costa Rica (McCain 2004) and Neotropical land birds (Rahbek 1997). Lack of correlation between species richness and altitude has also been reported, but more often for organisms that operate on a more fine grain scale, e.g. fungal wood decomposers (Meier et al. 2010) and microorganisms that follow pH more than climatic variables (Fierer et al. 2011). One suggestion for the discrepancies among trends is that altitudinal gradients span many biotopes and that the unique species communities occurring within biotopes are likely then to influence diversity patterns (Rahbek 1997). Accordingly, we restricted the present study to montane ecosystems rather than sampling a more complete altitudinal gradient that would include the Amazonian lowlands and adjacent lower Andean slopes.

Carabid beetle communities have been the focus of numerous ecological studies, mostly from temperate forests (Hosoda 1999; Eyre et al. 2005). In any assessment of biodiversity it is important to accurately sample and estimate total species richness of the focal taxon within a defined area (Coddington et al. 1991). However, sampling for most carabid beetle studies has been restricted to short time periods with incomplete seasonal sampling (Lövei & Sunderland 1996). In tropical forests, systematic carabid beetle sampling has primarily been at lower altitudes (Erwin 1991; Lucky

et al. 2002) with most studies lasting less than a few months, or random months across several years. The present study expands on the first survey of carabid beetles conducted in a tropical montane forest throughout an annual cycle and at multiple altitude zones.

Our primary focus was to look for assembly patterns for these beetles by estimating species diversity and community composition along an altitudinal gradient in montane Andean forests, with repeated sampling in both the rainy and dry seasons. Based on the increasingly harsh climate and increasingly simple biotic and abiotic environment as altitude increases, we predicted that carabid beetle species diversity will decrease with elevation, coupled with a change in carabid beetle species assemblages, due to turnover of species with different life history strategies with increasing altitude. Since precipitation and humidity decrease in the dry season (Rapp & Silman 2012), and low humidity has often been shown to be a limiting factor for carabid beetle diversity (Lövei & Sunderland 1996), we also predicted that seasonality would impact diversity.

Materials and methods

Collections of Carabidae

Carabid beetles were collected in K'osñipata Valley, within the Cultural Zone of Manu Biosphere Reserve, Department of Cusco, in southeastern Peru. Sampling sites and collection methods reported by Maveety et al. (2011) are corrected here due to new information: approximately 500 m intervals from 1400 m (not 1500 m) to 3400 m, using both active (hand searches) and passive (pitfall trap) collection techniques. It is important to note that these collection techniques primarily sampled adult epigeic carabid beetle assemblages.

Pitfall traps were collected, with the contents of each cup drained and passed through a fine mesh strainer, approximately every 30 days, from September 2007 to July 2008. Active hand searches were performed at night, and on the same dates as the trap collections. Collections spanned both seasons, rainy and dry. In the K'osñipata Valley, rainy months occur from November to April, with dry months from May to October; however, precipitation is greater than evapotranspiration for all months, and dry season months receive less rainfall (Rapp & Silman 2012).

Identifications were made to the level of morphospecies as presented in Maveety et al. (2011). We realize this is a simplified, imperfect approach. However, we believe that morphospecies classification represents a reasonable trade-off between absolute taxonomic accuracy (which may take many years to achieve) and the generation of comparative estimates of species diversity

for carabid assemblages for different elevations and for wet and dry seasons. It is important to note that initial identifications have been revisited and revised since the publication of Maveety et al. (2011), e.g. genera *Trechischibus* and *Paratrechus* had been misidentified and are now corrected, with the number of individuals for each revised.

Species accumulation curves

Smoothed species accumulation curves were constructed with 500 randomizations using the Mao Tau richness estimator, which estimates the number of species expected based on the total sampled assemblage (EstimateS 9, Colwell 2013). Species accumulation curves were used to interpolate, or rarefy, species numbers by sampling effort (i.e. number of individuals). Rarefied richness values are presented as means ± standard deviation, and the difference in means of rarefied richness for seasonal and altitudinal analysis was compared using *p*-values calculated in R 2.13.1 (www.r-project.org).

Diversity and community indices

Fisher’s alpha, non-parametric diversity indices, Shannon Wiener and Shannon’s evenness, and the

Berger Parker index (dominance) were calculated to further elucidate diversity patterns for both seasonal and altitudinal diversity. Species turnover between seasons and by altitude was calculated by Sørensen’s dissimilarity index (beta diversity). See Magurran (2004) for more detailed descriptions of these indices.

Ordination

Species composition by altitude and by season was analyzed via Non-metric Multidimensional Scaling (NMDS), using PC-ORD Version 6 (www.pcord.com). NMDS was calculated based on Sørensen’s index, using 500 runs with real data and 100 iterations; three dimensions were analyzed and the two dimensions with greatest *r*² values are reported in the results.

Results

Species diversity

A total of 1958 carabid beetles representing 72 morphospecies were collected. Although the majority (62%) of individuals were collected during the dry season (Tables 1, 2), the rarefied number of species (*S_r*) was significantly higher in the rainy season (62 ± 5.6) than the dry season (40 ± 3.7) (*p* = 0.0004, Figure 1). The

Table 1. Comparison of total number of carabid beetle morphospecies by tribe, collected with pitfall traps and by hand, between altitudinal zones and seasons at K’osñipata Valley, Peru from September 2007 to July 2008.

Morphospecies	Dry					Rainy					Total
	1400	2000	2500	2900	3400	1400	2000	2500	2900	3400	
BEMBIDIINI											
<i>Bembidion</i> A		2	3	5			1	2	9		22
<i>Bembidion</i> D				1						2	3
<i>Bembidion</i> E			3	15					2	5	25
<i>Bembidion</i> F		10									10
<i>Bembidion</i> G		1							1		2
<i>Bembidion</i> H		7	1								8
<i>Bembidion</i> I			10								10
<i>Bembidion</i> K		3					3				6
<i>Bembidion</i> L					22				1	3	26
<i>Bembidion</i> M									6		6
CICINDELINAE											
<i>Pseudoxycheila</i> <i>lateguttata peruviana</i>		4					1				5
GALERITINI											
<i>Galerita</i> A	2	3	10					13			28
<i>Galerita</i> B	1					2					3
<i>Galerita</i> C							1				1
<i>Galerita</i> D							2				2
HARPALINI											
<i>Goniocellus</i> A								1			1
<i>Notiobia</i> A	2										2
<i>Notiobia</i> B	2					1					3
<i>Notiobia</i> C	1					17					18
<i>Notiobia</i> D	2					1					3
<i>Notiobia</i> E	1	4				2					7
<i>Notiobia</i> F		5				2	11				18

(Continued)

Table 1. (Continued).

Morphospecies	Dry					Rainy					Total
	1400	2000	2500	2900	3400	1400	2000	2500	2900	3400	
<i>Notiobia</i> H	2					1					3
<i>Notiobia</i> I	213	1				41	7				262
<i>Notiobia</i> J						1					1
<i>Notiobia</i> K		1					1				2
<i>Pelmatellus</i> A		1									1
<i>Pelmatellus</i> B				5					4		9
<i>Pelmatellus</i> C		19	174	27			11	27	17		275
<i>Pelmatellus</i> D				1				1			2
<i>Pelmatellus</i> E								1			1
<i>Pelmatellus</i> F	2										2
<i>Pelmatellus</i> G	1										1
<i>Pelmatellus</i> H			70	138				21	55		284
<i>Pelmatellus</i> I	6					1					7
<i>Pelmatellus</i> J					63					1	123
<i>Pelmatellus</i> K		7					8				15
<i>Pelmatellus</i> L								1	1		2
<i>Selenophorus</i> A	6					6					12
<i>Trichopselaphus</i> A	6					3					9
<i>Trichopselaphus</i> B						1					1
LACHNOPHORINI											
<i>Anchonoderus</i> A		11					1				12
<i>Anchonoderus</i> B		1				1					2
<i>Pseudophorticus</i> A	10	4				1	4				19
LEBIINI											
<i>Calleida</i> A		3									3
<i>Calleida</i> B	1										1
<i>Lebia</i> A									1		1
<i>Lebia</i> B						1					1
OODINI											
<i>Dercylus</i> A						1					1
OZAENINI											
<i>Pachyteles</i> A	2					2					4
<i>Pachyteles</i> B						2					2
<i>Pachyteles</i> C						1					1
PERIGONINI											
<i>Diphloharpus</i> A		1									1
PLATYNINI											
<i>Dyscolus</i> A			1	166				9	196	9	381
<i>Dyscolus</i> B			2	9				8	10		29
<i>Dyscolus</i> C			1	3					3	1	8
<i>Dyscolus</i> D					2			2	4	5	13
<i>Dyscolus</i> E								1			1
<i>Dyscolus</i> G			2	1					1		4
<i>Dyscolus</i> H			1								1
<i>Dyscolus</i> J							3				3
<i>Dyscolus</i> L										1	1
<i>Dyscolus</i> M									1		1
<i>Glyptolenus</i> A		40	2				7	12	1		62
<i>Platynus</i> A		21					12				33
PTEROSTICHINI											
<i>Loxandrus</i> A						1					1
<i>Loxandrus</i> B						1	1				2
<i>Pseudobarys</i> A		1									1
<i>Trichonilla</i> A						1					1
SCARITINI											
<i>Ardistomus</i> A						4					4
TRECHINI											
<i>Paratrechus</i> C			1	68					69		138
<i>Trechischibus</i> A				3					2		5
Total no. of beetles	260	150	281	442	87	95	74	99	385	85	1958
Total no. of species	17	22	14	13	3	24	16	13	20	8	72

Table 2. Carabid beetle diversity and dominance indices by season and altitude at K'osñipata Valley, Peru from September 2007 to July 2008.

	No. individuals	No. species	Shannon Wiener	Shannon's evenness	Fisher's alpha	Dominance	Beta diversity
<i>Season</i>							
Rainy	738	60	2.834	0.687	16.24	0.27	0.362
Dry	1220	51	2.589	0.649	11.62	0.183	
<i>Altitude (m)</i>							
1400	355	29	0.84	0.19	7.14	0.72	
2000	224	26	2.62	0.6	8.4	0.21	0.786
2500	380	20	1.66	0.38	4.78	0.53	0.796
2900	827	22	0.81	0.19	3.94	0.42	0.476
3400	172	8	1	0.23	1.49	0.69	0.643

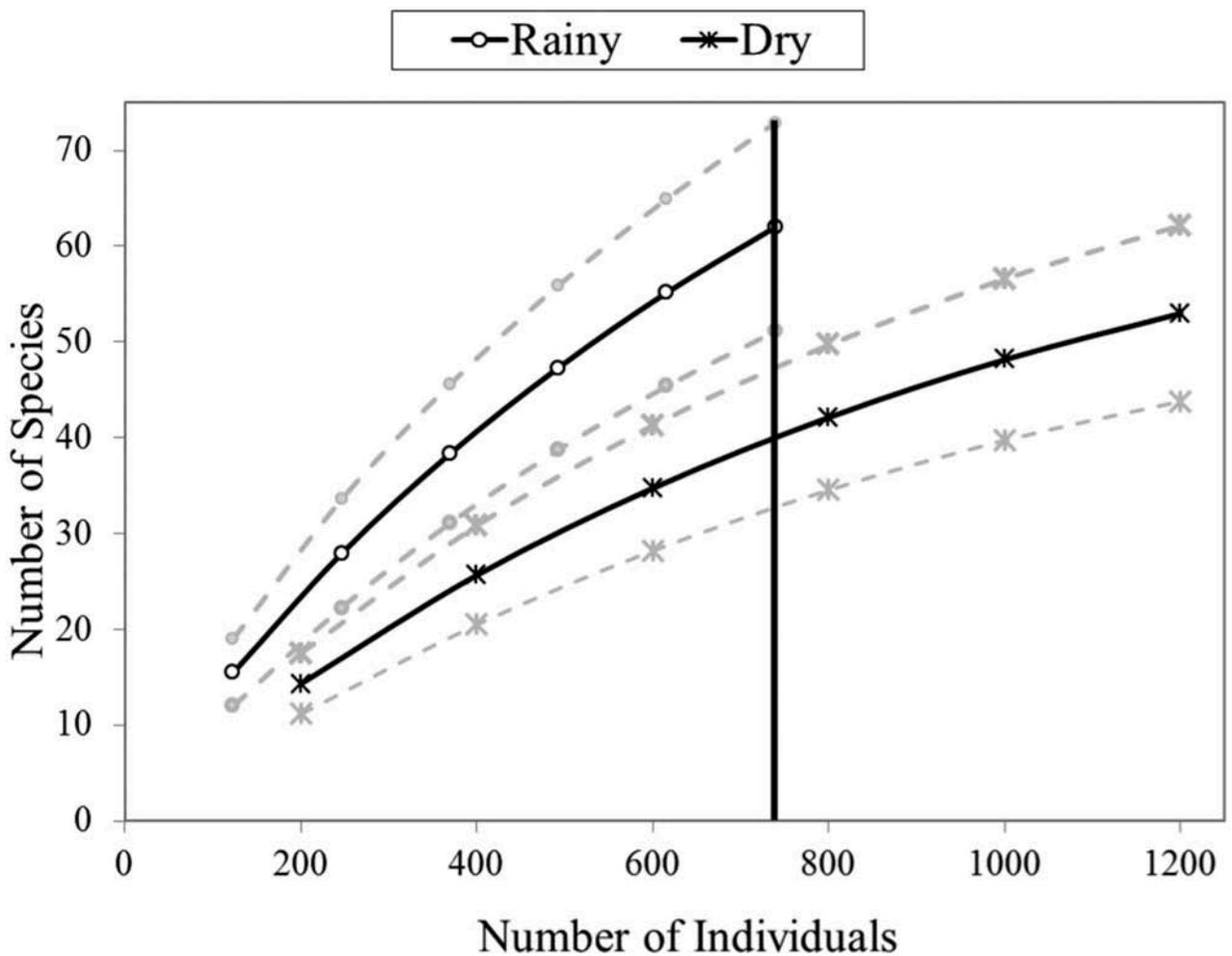


Figure 1. Species accumulation curves for carabid beetles collected in the rainy season (November 2007–April 2008) and the dry season (May–October 2008) at elevations between 1400 and 3400 m at K'osñipata Valley, Peru. Species numbers were estimated using the Mao Tau richness estimator. Vertical line represents a rarefied sample size of 739 individuals; dashed lines represent 95% CI.

higher values for diversity indices (i.e. Shannon Wiener, Shannon's evenness, and Fisher's alpha) and dominance also occurred during the rainy season (Table 2).

Species accumulation curves for the five altitudinal sites are presented in Figure 2A. No species

accumulation curve reached an asymptote, although at 2900 m and 3400 m a relatively small increase in sample size might result in an asymptote. In contrast, the slopes of the lower altitude curves remain nearly constant, even as sample size increases. Figure 2B

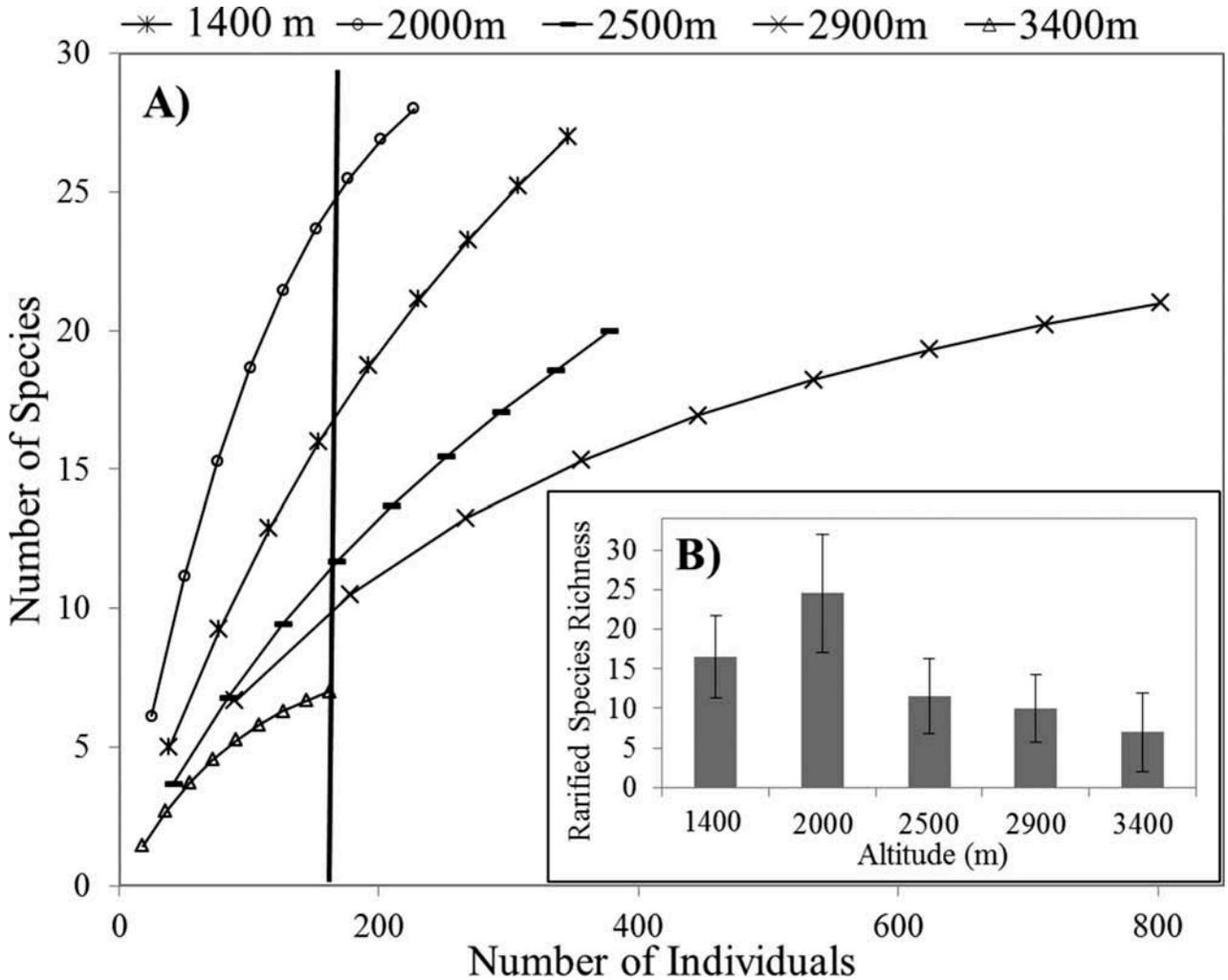


Figure 2. Number of carabid species collected at K’oshiyata Valley, Peru, as a function of (A) species accumulation, using the Mao Tau richness estimator, for each altitudinal zone (the vertical line represents a standardized sample size where $N = 172$ [95% CI are not included for clarity]); and (B) rarified richness and altitude, adjusted by standardized sample size. Bars represent 95% CI.

depicts S_r (adjusted by the Mao Tau estimator and derived from the species accumulation curves) for each altitude. S_r varied significantly among all sites ($G = 12.9, p < 0.05$), and peaked at 2000 m [2000 m \neq 1400 m ($p = 0.0498$) and 2000 m \neq 2500 m ($p = 0.0024$)], but there was no difference in S_r for sites ≥ 2500 m. There was no significant linear or curvilinear correlation between S_r and altitude.

The highest values for Shannon Wiener diversity, Shannon’s evenness, and Fisher’s alpha occurred at 2000 m (Table 2), but dominance was lowest at 2000 m. Fisher’s alpha is one of the more useful indicators of community diversity because of its independence of sample size, as evidenced by lack of correlation between the number of individuals and Fisher’s alpha value ($r = 0.0096, p = 0.875$). Furthermore, as indicated in Table 2, the 2500 m and 2900 m altitudinal

zones were the most compositionally similar (Sørensen’s dissimilarity index = 48%), with the greatest species turnover at the next lower altitudinal zone, between 2000 m and 2500 m (Sørensen’s dissimilarity index = 80%).

Community composition

Altitude, as indicated by NMDS, has a pronounced effect on species composition (Figure 3). Since the data points of the different seasons did not cluster in any clear pattern there was no apparent seasonal effect. This is reinforced by the low beta diversity, 36% dissimilar assemblages (Table 2), the relatively low level of species overlap between seasons, with 17% of morphospecies unique to the dry and 28% unique to the rainy season. Axes 2 (x-axis) and 3 (y-axis) explained the greatest

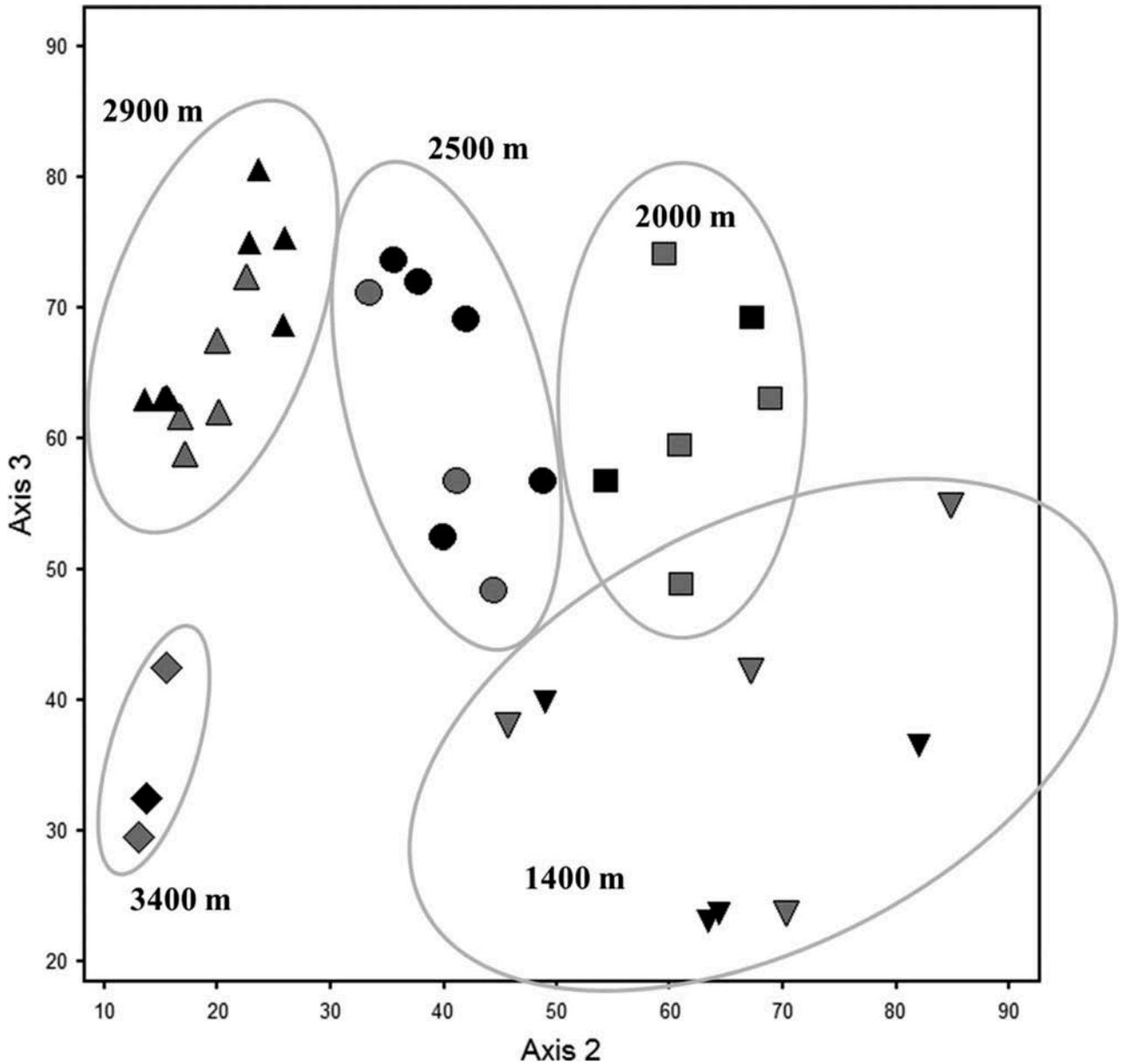


Figure 3. Ordination by non metric multidimensional scaling based on Sørensen’s Index (Bray Curtis). Each data point represents the carabid beetle assemblage within an altitudinal zone (indicated by clusters). Black fill represents dry season month and gray fill represents rainy season months.

amount of variability ($r^2 = 0.144$ and 0.131 , respectively), with Axis 2 likely including an altitudinal effect since the points are arranged by descending altitude. The greatest morphospecies variability within an altitudinal zone occurred at 1400 m, which also had the highest proportion of unique species (32%). The 2000 m zone also had a relatively high proportion (21%) of unique species. In contrast, the upper three altitudinal zones each had less than 4% unique species. The lower two altitudinal zones included two tribes, Galeritini and Lachnophorini, which were not found at or above 2500 m. Additionally, Bembidiini and Trechini, both tribes

typical of high altitude environments, were not found below 2000 m (with Trechini only occurring at the 2500 m and 3000 m zones).

Discussion

Seasonality

Seasonality is an important component of most biodiversity assessments. If the goal of a biodiversity study is a complete inventory of a specific higher taxon, a researcher should not only decide where

(e.g. altitudinal gradient, physical location) and how (e.g. collection methods) to optimize the number of species sampled, but also when (e.g. time of year) collections should take place. Within the montane forests of the Peruvian Andes, we found a significantly higher number of species in the rainy season than during the dry season. Similar results were observed for insect species in the tropical lowlands of Costa Rica and Caribbean (Janzen 1973) and for Coleoptera in the Canal Zone of Panama (Erwin & Scott 1981). The increase in species number for our study could be related to compositional turnover, because communities were no more than 64% similar between seasons. Given the results of our study, we recommend that biodiversity studies include collections made during the rainy *and* dry seasons, with collections conducted periodically throughout each season.

The effects of inter-annual variation on carabid species diversity and community composition in the tropics are virtually unknown, and future studies will be needed to assess inter-annual variability. Erwin et al. (2005) found that three years of fogging (nine total sampling events) produce an asymptotic accumulation curve for carabid beetles in the lowland rainforest canopies. Because the collection methods of the present study, i.e. pitfall traps and hand collections, yield lower abundances, we suggest that at least five years would be needed to compare inter-annual patterns with confidence. Erwin et al. (Forthcoming) provide data from trans-seasonal and trans-annual canopy samples in the western Amazon of Ecuador that indicate the Southern Oscillation Index (SOI), a measure of occurrence and strength of El Niño and La Niña, may be associated with major swings in species abundances when marked by La Niña events. Ideally, studies in the tropics and subtropics should report the SOI indices for the study period. Following that suggestion, the SOI values (available at <http://www.cpc.ncep.noaa.gov/data/indices/soi>) indicate no pronounced oscillation during our collecting period.

Altitudinal gradient

Carabid species assemblages appear to be strongly influenced by altitude in Neotropical Peruvian cloud forests. Altitudinal zones were distinct in the ordination space, with only slight overlap between the 1500 m and 2000 m zones. Adjacent altitudinal zones along the gradient were no more than 52% similar. The 3400 m altitudinal zone, which was localized in the ordination space, is where cloud forest and elfin forest meet the Puna alpine grassland ecosystem. Only one species was unique to this zone; the remaining seven

species had altitudinal ranges that did not reach below 2500 m. Turnover in species composition along the altitudinal gradient is probably linked to the different environmental adaptations necessary for increasingly harsh abiotic environments and decreases in primary productivity (McCoy 1990; Escobar et al. 2005). Changes in tree species composition for this same gradient (Meier et al. 2010) are likely to influence the composition of carabid beetle assemblages, or at least point to the influence, such as different soil types. Changes in predation pressures could also possibly influence carabid beetle assemblages. In the K'osñipata Valley of southeastern Peru, where this study was conducted, birds and bats, both potential predators of carabid beetles, exhibit altitudinal differences in species composition (Patterson et al. 1998). Although no potential biotic causal agents are identified, dung beetle assemblages also vary significantly between high and low altitude locations in the Colombian Andes (Escobar et al. 2005).

Rarified richness of carabid beetles suggest that there could be a mid-elevation peak in diversity within the cloud forest zone (with S_r highest at the mid-elevation site, 2000 m). The altitudinal zone 2000 m is situated just above cloud base in the K'osñipata Valley, representing the approximate location of the ecotone between lowland forest and high Andean forest (Young & León 1999). The high beta diversity value indicates that these assemblages are relatively unique, with the highest dissimilarity (80%) for assemblages between 2000 m and 2500 m. A middle altitude peak in species richness has been reported for other Neotropical insect taxa, e.g. geometrid moths in Costa Rica (Brehm et al. 2007), scarab beetles in the Colombian Andes (Escobar et al. 2005), ichneumonid wasps along the same gradient as this study (Castillo-Cavero 2009), and sweep samples of insects in Venezuela (Janzen et al. 1976). Moret (2009) also observed a mid-elevation peak in carabid beetle species within the alpine Páramo ecosystem in Ecuador, but like in the present study his lower elevation was not in the lowlands of Amazonia. The mid-domain effect (MDE) has been offered as an explanation for the mid-elevation peak in species diversity (e.g. McCain 2007). The MDE predicts that species richness will peak at the middle of a bounded gradient because there is a higher probability that species will occur at the center of the gradient due to geometric constraints (Colwell et al. 2004). However, the MDE hypothesis may better explain patterns for data drawn from a more complete altitude gradient. For ground dwelling carabids, that should include sampling of beetle assemblages beginning in lowland Amazonia, whereas in this study sampling did not occur at less than 1400 m. For example, with more extensive

search efforts, Erwin (1991) found more than 1000 ground dwelling and arboreal carabid species at Pakitza (Rio Manu, Peru); also, nearly 500 arboreal carabid species have been found from arthropod canopy fogging in the Yasuni area of Ecuador (Erwin et al. 2005), with the ground fauna sampling still underway.

Although a middle peak in species richness has been documented for some Neotropical taxa, a decreasing monotonic trend with altitude in species richness has also been reported, e.g. syntopic birds in Peru (Terborgh 1977), termites in Peru (Palin et al. 2011), and Neotropical tree communities (Gentry 1988). Raw species counts for carabid beetles used in this study also decrease monotonically (Maveety et al. 2011). Wolda (1987) suggested that a linear trend in species richness may be linked to long term sampling while short term sampling is more likely to reveal a middle altitude peak.

Estimates of species richness by altitude may depend on the type and length of sampling employed. The present study was limited to one collection year on one transect and did not extend to the lowest altitudes. Given the range of altitude we sampled, which focused on the high altitude montane ecosystem, we cannot definitively predict the pattern of diversity if sampling was extended to the low point in the Amazon basin in Manu National Park (approximately 300 m elevation). Sampling multiple transects spanning the entire altitudinal gradient would also be needed to obtain a complete picture of how species richness varies with altitude (Rahbek 1995). However, this study is the first systematic investigation of carabid beetles over an annual cycle and at multiple elevations of a tropical montane forest. The results indicate that tropical montane species assemblages change considerably with altitude and season. Additional studies are needed to document the full extent of these changes, and could be especially relevant in light of the potential effects of climate change (Williams et al. 2007).

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