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Species Richness and Phenology of Butterflies along an Altitude Gradient in the Desert of Northern Chile

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ABSTRACT

We use butterfly data from an arid subtropical elevation gradient to test temperate-zone hypotheses regarding altitude effects on diversity and phenology. Specifically, species richness is predicted to peak at mid-altitude on arid-zone mountains with opposite temperature and precipitation gradients, and phenological windows of activity are expected to be more synchronized, shorter, and later with altitude.

A transect on the Pacific slope of the Andes in northern Chile (23°S, 2400–5000 m a.s.l.) was observed fortnightly between October 2008 and June 2009. The 13 species observed showed high altitudinal and temporal turnover, dividing the transect into three entomofaunal zones that follow well-documented altitudinal vegetation belts. Species richness peaked at mid-altitude in the Puna shrub belt, the zone with highest plant productivity and diversity, supporting McCain's water-temperature hypothesis. Community-level predictions about phenology were not met: instead, the flight period began earlier at high altitude, presumably due to earlier water availability, and neither synchronization nor duration of flight periods varied consistently with altitude. At the species level, relationships between butterfly phenology and altitude were variable, suggesting no direct effect of altitude but rather complex effects of changing environmental conditions that vary according to individual species' ecological requirements, host plant use, and lifecycle.

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Introduction

Ecological gradients that occur with increasing latitude are well-documented, and similar patterns are often expected with altitude, namely, that as elevation increases, species richness should decrease and phenological windows of activity be shorter, later, and more synchronized (Rahbek, 1995; Brown and Lomolino, 1998). However, empirical studies show that a variety of different patterns can exist: species richness sometimes increases and sometimes decreases with altitude, and the most common pattern involves a richness peak at mid-elevation (Grytnes and McCain, 2007). For instance, in the tropical Andes, the diversity of butterflies (Pyrcz et al., 2009) and of geometrid moths (Brehm et al., 2007) peaks at mid-elevation.

Similarly, although theoretical work suggests that the phenological window of opportunity should be later and shorter with increasing altitude (Scott, 1987; Boggs and Murphy, 1997; Hodkinson, 2005), this has only been supported by a few studies in the temperate zone, showing, for example, that the timing of flowering is later with increasing elevation (Arroyo et al., 1981) and that the flight period of butterflies is later, shorter, and more synchronized among species (Shapiro, 1975; Gutiérrez and Menéndez, 1998; Ashton et al., 2009; Gutiérrez-Illan et al., 2012). However, as early as 1920, Verity (1920) showed that altitudinal gradients can elicit far more complex phenological patterns and concluded that these depend on local environmental conditions rather than altitude per se.

Indeed, many different environmental drivers can be associated with altitude depending on the context. The factors that consistently vary with altitude in the same way are land area, atmospheric pressure, temperature, clear-sky solar radiation, and proportion of radiation as UV-B. Many other factors such as precipitation, cloud cover, wind velocity, and seasonality often show relationships with altitude, but these are not predictable, they can be positive, negative, or peak at mid-elevation (Körner, 2007). Therefore, the ecological effects of increasing elevation can be highly variable, depending on how these factors vary with altitude.

For instance, it has been suggested that species richness tends to decrease with altitude in high-moisture tropical regions, but to peak at mid-altitude in temperate mountains with an arid climate at the base and increasing precipitation with altitude (McCain, 2007). This author suggests that the western slope of the desert Andes is an ideal test of this model, since it is found at tropical latitudes but has an arid climate with increasing precipitation at higher altitude and hence permits separation of the effects of latitude and of aridity. McCain (2007) used partial bat data from Peru as preliminary support for this model, suggesting that diversity does indeed peak at mid-altitude in this tropical but arid climate.

The present study examines altitude effects on diversity and phenology of butterflies in a sub-tropical region with a strong positive altitudinal precipitation gradient, the Andean Pacific slope in the Atacama desert of northern Chile. The Pacific slope of the central Andes in the IInd region of northern Chile ranges from the Salar de Atacama (2400 m a.s.l.) to the altiplano (5000 m). Precipitation occurs in the austral summer coming over the cordillera and is therefore earlier and more abundant at higher altitude. Opposing temperature and humidity gradients lead to the formation of well-defined altitudinal vegetation belts (Villagrán et al., 1981). This trade-off between increasing precipitation and decreasing temperature with altitude is generally held responsible for the well-documented peak in plant cover and diversity in the mid-altitude Puna shrub belt (Arroyo et al., 1988; Squeo et al., 1994).

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Based on the model proposed by McCain (2007), we predict that species richness should peak at mid-elevation, in the Puna belt. Elevational trends in phenology have only been examined in the temperate zone (Shapiro, 1975; Gutiérrez and Menéndez, 1998; Ashton et al., 2009; Gutierrez-Illan et al., 2012), where findings suggest that flight periods should be later, shorter, and more synchronized at higher elevations.

Methods

ALTITUDINAL TRANSECT

The transect followed the private road to the ALMA radio-observatory (http://www.almaobservatory.org) near San Pedro de Atacama between 2400 and 5000 m a.s.l. Six stations were established along the transect, at 3000 m (23°4′31.07″S, 67°58′16.51″W), 3300 m (23°4′7.73″S, 67°55′48.22″W), 3600 m (23°4′5.74″S, 67°53′57.28″W), 4100 m (23°3′19.77″S, 67°52′27.85″W), 4500 m (23°2′18.48″S, 67°50′37.13″W), and 4850 m (23°0′44.55″S, 67° 48′10.22″W) in order to represent the main vegetation belts.

The altitudinal vegetation belts of northern Chile have been well characterized in several studies carried over a latitudinal range encompassing our study area (Villagrán et al., 1981; Villagrán et al., 1983; Arroyo et al., 1988, 1998; Latorre, 2002). The first station on our transect (at 3000 m a.s.l.) is located in the pre-Puna belt, the hottest and most arid zone, where precipitation averages less than 50 mm per year. This vegetation belt is characterized by cacti (*Maihueniopsis camachoi* [Cactaceae]) and xerophyllic shrubs, including *Atriplex imbricata* [Chenopodiaceae], *Ambrosia artemisioides* [Asteraceae], *Ephedra breana* [Ephedraceae], *Haplopappus rigidus* [Asteraceae], and *Krameria lappacea* [Krameriaceae]. The site at 3300 m is still within the pre-Puna belt, with vegetation mostly dominated by cacti (*Echinopsis atacamensis* and *Maihueniopsis camachoi* [Cactaceae]) and shrubs (*Fabiana ramulosa* [Solanaceae], *Ephedra breana* [Ephedraceae], *Atriplex imbricata* [Chenopodiaceae], and *Ambrosia artemisioides* [Asteraceae]).

At the 3600 m station begins the Puna belt, dominated mostly by shrubs, including *Fabiana denudata*, *F. ramulosa* (Solanaceae), *Chuquiraga atacamensis* (Asteraceae) and *Adesmia melanthes* (Fabaceae). This is also the zone of highest plant cover and diversity. The site at 4100 m is in the transition between the Puna shrub belt and the grass-dominated Andean steppe, and is dominated by tussock grasses (*Festuca orthophylla* [Poaceae]), cacti (*Maihueniopsis boliviana* [Cactaceae]), shrubs (*Baccharis tola* and *Parastrephia quadrangularis* [Asteraceae], *Junellia seriphioides* [Verbenaceae], *Adesmia melanthes* [Fabaceae]), and annuals (*Descurainia myriophylla* [Brassicaceae] and *Lupinus subinflatus* [Fabaceae]).

The high Andean steppe at the 4500 m station is dominated primarily by tussock grasses (*Festuca orthophylla* [Poaceae], *Deyeuxia curvula* [Poaceae]) and secondarily by cushion plants (*Pycnophyllum bryoides* [Caryophyllaceae], *Urbania pappigera* [Verbenaceae], *Werneria glaberrima* [Asteraceae]), and small cushion-forming shrubs (*Mulinum crassifolium* [Apiaceae], *Senecio puchii* [Asteraceae]). Finally, the 4850 m station is in the Subnival zone, where the grasses and shrubs dwindle in importance, while cushion plants continue to predominate (*Xenophyllum poposum* [Asteraceae], *Pycnophyllum bryoides* [Caryophyllaceae], *Urbania pappigera* [Verbenaceae]) and small annuals (*Menonvillea virens* [Brassicaceae]) become more common. At this altitude, summer monsoon precipitation is more abundant (around 250 mm per year) and often falls as snow, which quickly sublimates under high daytime temperatures.

OBSERVATIONS

Weekly observations based on Pollard (1977) were conducted between October 2008 and June 2009 at the six transect stations. Observations consisted of walking a predefined circuit at each site for 30 min and recording all butterflies seen. Butterflies are mainly seen between about 1100 and 1500 hours, due to extreme daily temperature variation (30 °C between the maximum in the early afternoon and the overnight minimum [Schmidt, 1999]). Onset of strong winds in the afternoon (Schmidt, 1999) generally signal the end of butterfly flight periods (Descimon, 1986). Some individuals were caught with nets to confirm species identification.

Temperature loggers (DS1922L Maxim's iButton) were placed at the six stations along the altitudinal transect. They were affixed on wooden signposts at 10 cm above the ground, on the south side of the signposts to minimize sun exposure. Temperature decreases sharply with elevation above the ground, due to radiant heat from the ground under strong insolation and the low thermal capacity of the arid air (Schmidt, 1999). Thermal sensors were placed low down because many butterflies, especially at higher altitudes, were observed flying at this level. These sensors continuously recorded temperature at 10 min intervals during the study period.

Plant names are given as per the International Plant Names Index (2010), published on the Internet (http://www.ipni.org) and butterfly names as per the Darwin Andean Butterfly Database (2010), at http://www.andeanbutterflies.org/database.html.

ANALYSIS

Species accumulation curves were calculated for each elevation. We calculated Mao Tau sample-based rarefaction curves using EstimateS software (Colwell, 2005; version 7.5) separately for each site. Butterfly species richness was plotted against altitude to examine the shape of the relationship and related to regional long-term temperature and precipitation data taken from Schmidt (1999).

We analyzed the degree of species sharing among butterfly assemblages among elevations (an inverse measure of turnover, or beta diversity). We used the abundance-based estimate of the Chao–Jaccard similarity measure, computed using EstimateS (Colwell, 2005; version 7.5) to build a dendrogram showing relationships between communities along the transect. This statistic is based on the probability that a butterfly randomly drawn from each of two samples will belong to a species that is shared between the communities, adjusted for undetected shared species.

The relationship between altitude and phenology was assessed by examining the overall abundance of butterflies at the different sites throughout the season. The midpoint and duration (in days) of the flight period for each species was compared between sites.

Results

SPECIES RICHNESS

In total, 509 individuals representing 12 species from 4 families were seen in 108 h of observation (see Table 1). This represents

TABLE 1

List of butterfly species observed. Identifications were made with the help of Peña and Ugarte (1996) and by consulting the collection at the Museo Nacional de Historia Natural (Santiago, Chile). Names are as per the Darwin Andean Butterfly Database (2010, http://www.andeanbutterflies.org/database.html) and distribution information from Peña and Ugarte (1996).

Species	Family	Distribution
Pyrgus barrosi E. Ureta1956	Hesperiidae	Puna endemic (highlands)
Pyrgus fides K.J. Hayward 1940	Hesperiidae	Widespread in Chile
Hypsochila wagenknechti sulfurodice E. Ureta 1955	Pieridae	Central Andean endemic
Phulia nymphula nymphula (C.E. Blanchard 1852)	Pieridae	Central Andean endemic
Pierphulia rosea rosea (E. Ureta 1956)	Pieridae	Puna endemic (highlands)
Tatochila mercedis macrodice O. Staudinger 1899	Pieridae	Puna endemic (highlands)
Madeleinea pelorias (G. Weymer 1890)	Lycaenidae	Puna endemic (valleys)
Strymon flavaria (E. Ureta 1956)	Lycaenidae	Puna endemic (valleys)
Leptotes trigemmatus (A.G. Butler 1881)	Lycaenidae	Widespread in Chile
Faunula leucoglene leucoglene C. Felder & R. Felder 1867	Nymphalidae	Central Andean endemic
Palmaris penai (K.J. Hayward 1967)	Nymphalidae	Puna endemic (highlands)
Vanessa carye (J. Hübner [1812])	Nymphalidae	Widespread in Chile

70% of butterfly species whose distribution range overlaps with our study area (Peña and Ugarte, 1996). Many of the other species are wetland specialists, whose habitat was not sampled.

Mao Tau species accumulation curves (Fig. 1) for all six sites show asymptotic trends, suggesting that all species present in these habitats were observed. These curves also show a peak in species richness per sampling effort at mid-altitude at the 4100 m site.

A plot of species richness against altitude shows a unimodal pattern (Fig. 2). Regional long-term temperature and precipitation data were also graphed on the same figure and show opposing altitudinal gradients, suggesting minimum physiological stress at intermediate altitudes.

Butterfly communities showed elevational turnover in species composition (Fig. 3). Only one species was found across most of the altitude range (*Vanessa carye*). We compared community composition among sites using the Chao-Jaccard abundance-based similarity estimator. We then grouped sites by community similarity using single-linkage cluster analysis and displayed the result as a dendrogram (Sanders, 2003). The dominant plant community was noted on the dendrogram to illustrate the relationship between changes in the butterfly community and changes in the dominant plant species present (Fig. 5). In general, sites that were farther apart in elevation (and in map distance) were less similar in composition. The level of compositional similarity was highest between the 3000 m and 3300 m site, between the 3600 m and the 4100 m sites, and between the 4500 and 4850 m sites (Fig. 5). These data suggest a turnover among three faunas defined by elevation.

PHENOLOGY

Figure 3 shows the abundance for each butterfly species at each of the six sampling sites throughout the season, along with temperature data from the sensors at each site, and precipitation estimated from a weather station near the top of the transect. The highest altitude sites show a strong spring abundance peak in October–November, followed by low numbers throughout the summer. The middle altitudes show a smaller spring peak, followed by a strong mid-summer peak in February. The lowest altitude site shows a strong spring peak in December, followed by a smaller summer peak in February–March. These community-level trends are difficult to interpret since they represent several species with very different flight times; however, they clearly do not fit the expectation of overall later, shorter, and more synchronized activity at higher altitude. Instead, activity begins earlier at higher altitude and is more pronounced in late summer at low altitude.

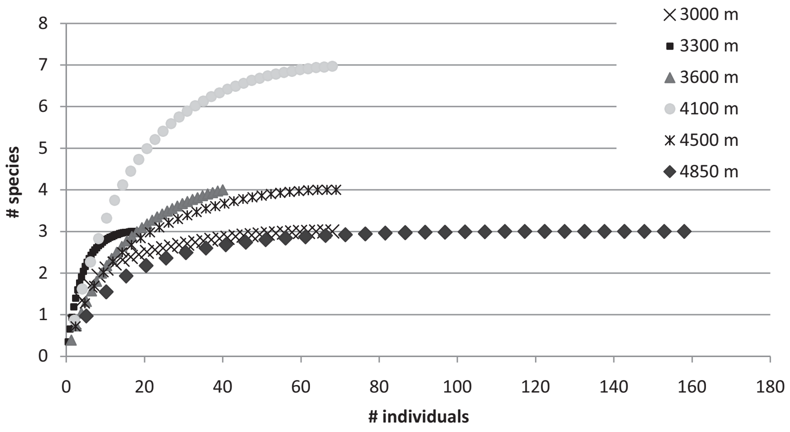

FIGURE 1. MaoTau species accumulation curves showing expected species richness versus sampling effort (number of individuals encountered). A separate curve is plotted for each site along the transect.

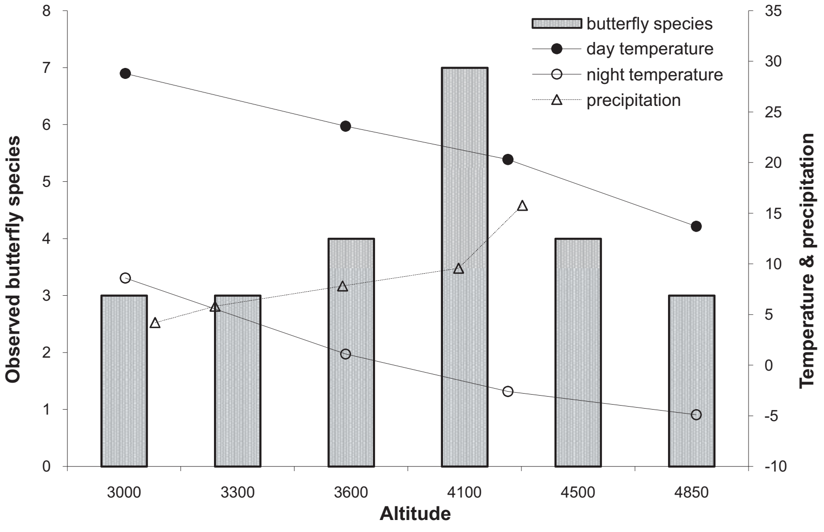

FIGURE 2. Butterfly species richness pattern along the elevational gradient. Temperature data is shown as December mean daily maximum and December mean daily minimum in °C, over the period 1991–1994 along an altitudinal transect 35 km north of our transect. Annual precipitation (in cm) data is from regional weather stations and is averaged over the period 1978–1985 and 1987–1988. Climate data is modified from Schmidt (1999).

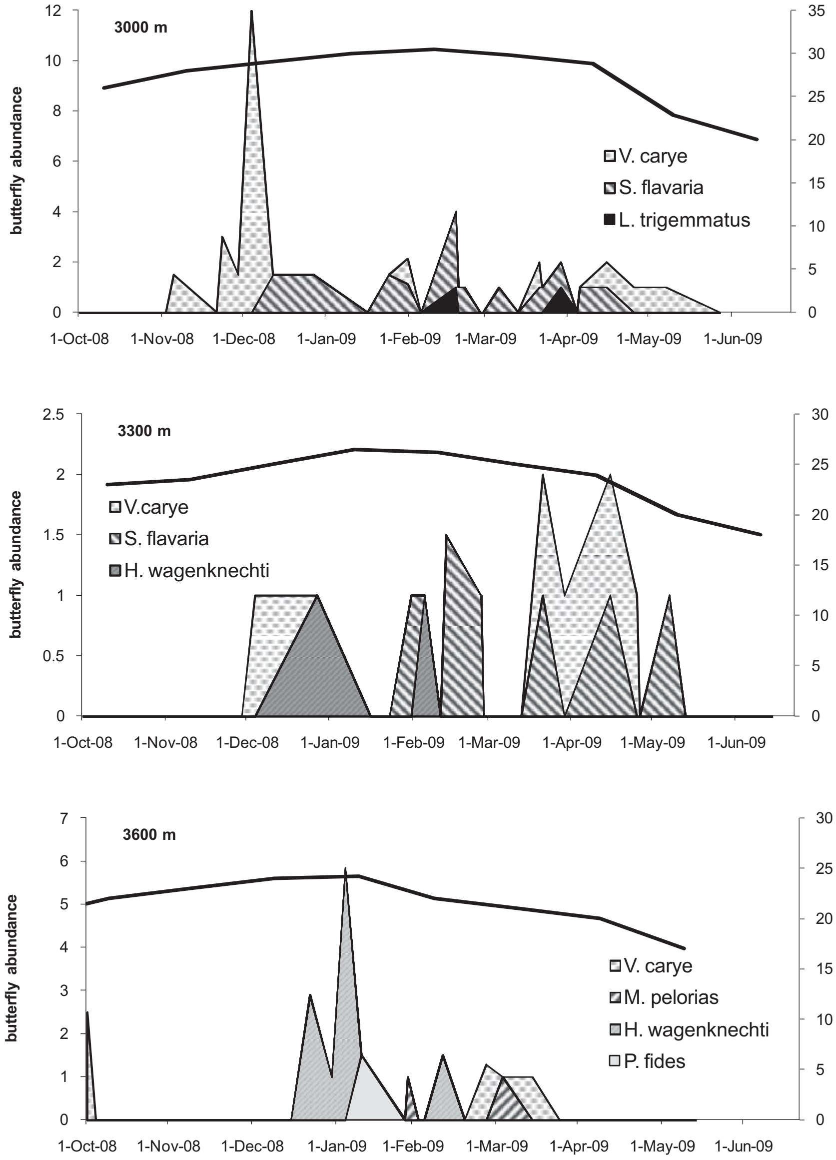

FIGURE 3. Butterfly abundance at each site between October 2008 and June 2009 (per 30 min. observation period). Temperature data (weekly average temperature between 1200 h and 1500 h from the sensor at 10 cm above the soil at each site) is shown in °C on the right-hand *y*-axis. The bottom panel also shows precipitation events, estimated from abrupt peaks in humidity data from the APEX radio telescope weather station (5000 m elevation, 3 km east of our sixth site).

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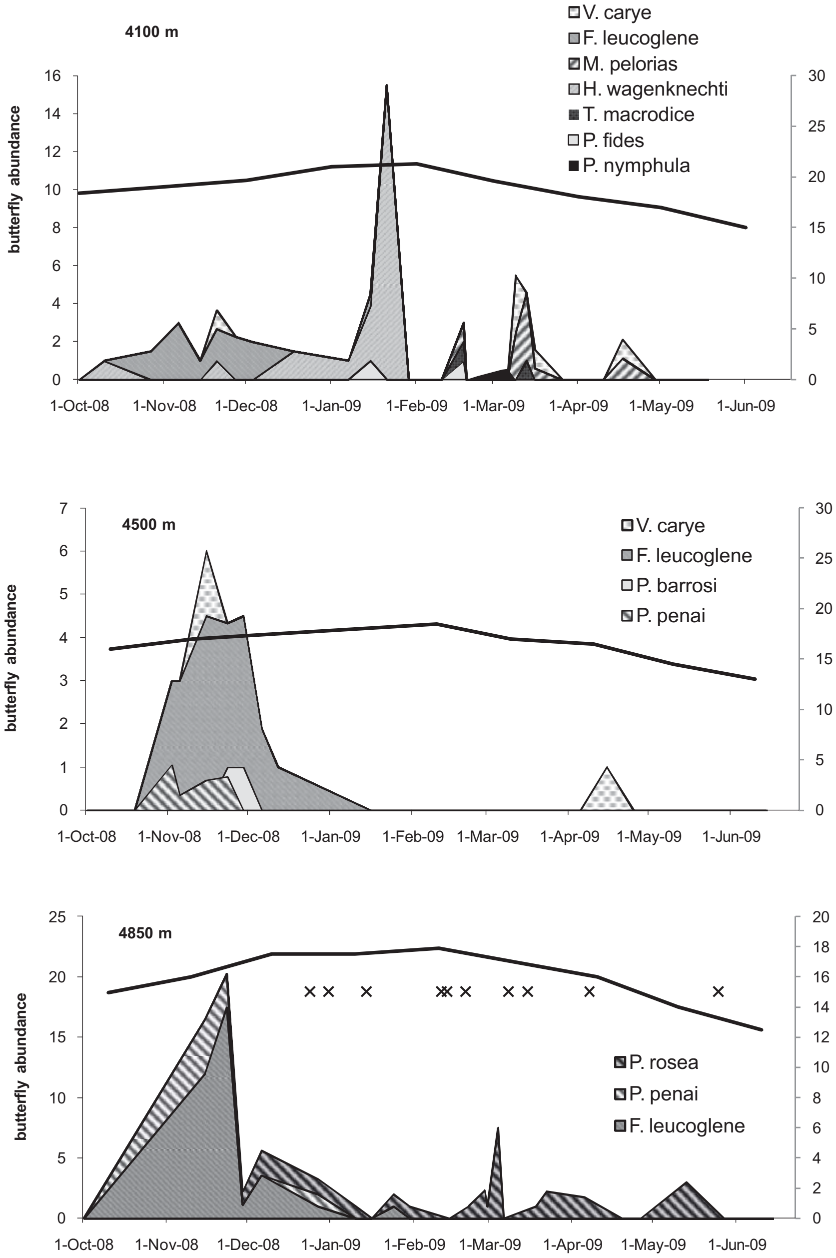

FIGURE 3. (*Continued*)

The average midpoint and duration of flight periods of each species at all six altitudes are shown in Figure 4. No clear overall pattern is apparent. Of the 7 species that are present at more than one station, one shows a later flight period at higher altitude (*Strymon flavaria*), 2 show earlier flight periods at higher altitudes (*Hypsochila wagenknechti* and *Madeleina pelorias*), and 4 show no clear change (*Vanessa carye*, *Pyrgus fides*, *Palmaris penai*, and *Faunula leucoglene*). There might be a pattern of earlier flight periods with increasing altitude in high-elevation species and the reverse in low-elevation species, but the number of species is too few for analysis. The mean duration of the flight period shows no clear relationship with altitude either. The species with by far the longest flight periods are *V. carye* which is present at all but the highest elevations, and *P. rosea* which is present only at the highest elevation. Four middle- to high-altitude species show longer flight periods at higher elevations (*H. wagenknechti*, *M. pelorias*, *P. fides*, *P. penai*), whereas one low-altitude species (*S. flavaria*) shows a shorter flight period with increasing altitude, and *V. carye* and *F. leucoglene* show no difference.

The flight period midpoint and duration can only be considered meaningful measures if flight takes place over a relatively short period of time with one seasonal peak (Gutiérrez and Menéndez, 1998). In the case of species with short uninterrupted flight periods, they likely represent a single generation (e.g. *P. penai*, *M. pelorias*). This is particularly true at the high-altitude sites where the relatively low temperatures imply a long larval development stage. Thus, the extended flight period of *P. rosea* likely represents polymodal emergence rather than multivoltinism, although this is impossible to test with our data. *V carye* is multivoltine in the temperate zone of the Andes exhibiting seasonal upland migration (Shapiro and Geiger, 1989; Peña and Ugarte, 1996). We show a similar pattern, as *V carye* was observed mostly at low altitudes in the spring, and then all along the altitudinal gradient in late summer (Fig. 3). *H. wagenknechti* has previously been reported to

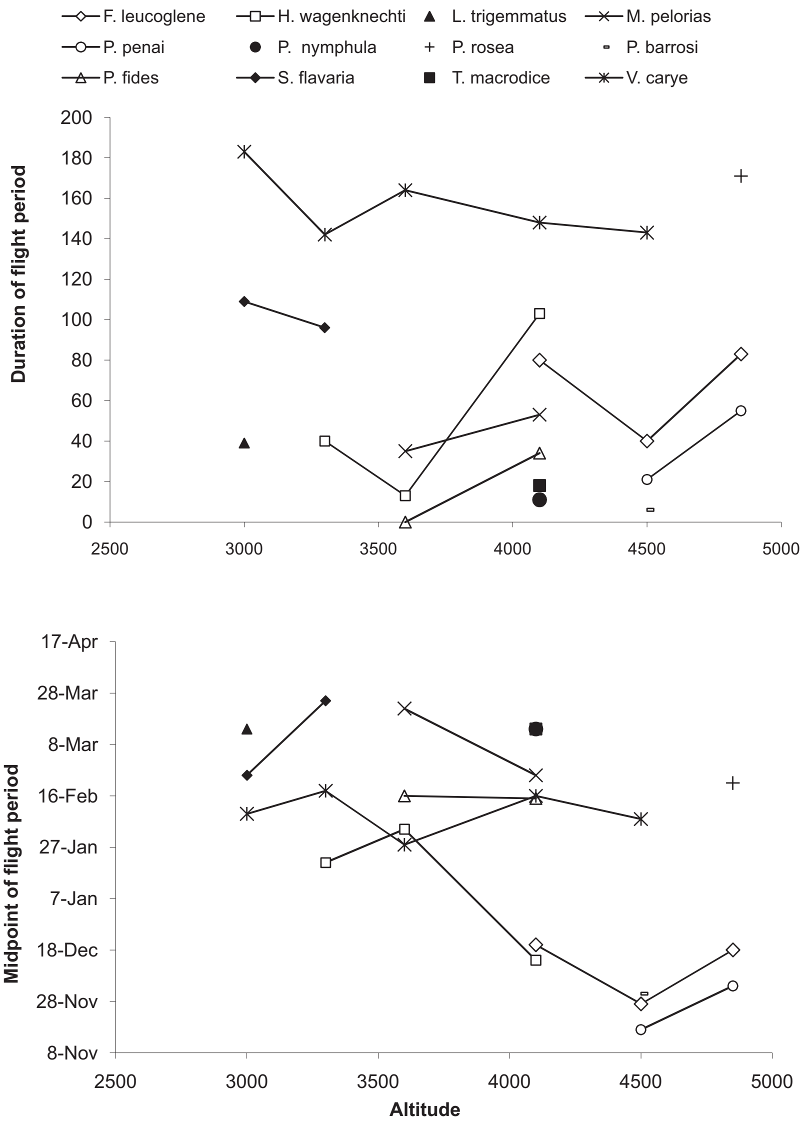

FIGURE 4. Mean midpoint and duration (in days) of the flight period of all species across the altitudinal gradient. Species found at only one site are represented by a point, whereas those found at several altitudes are represented by lines joining those points.

show two generations per year farther south in the temperate Andes: one small peak in October and a larger one in the summer (Courtney and Shapiro, 1986), similar to the pattern observed at our 4100 m site. *T. m. macrodice* migrates upland seasonally over two or three generations per year in Argentina (Shapiro, 1989) but was only observed occasionally during a short period in the present study.

Discussion

ALTITUDINAL PATTERNS OF SPECIES RICHNESS

Our data suggest that butterfly species diversity peaks at mid-altitude at the interface between the Puna shrub belt and the Andean steppe, due to the overlap between high-altitude and mid-altitude species (Fig. 3). This supports McCain's (2007) hypothesis that mid-altitude peaks should be expected in mountain ranges with inverse temperature and precipitation gradients. This hypothesis has received support from data on small mammals, bats, and birds, but not reptiles; it appears that reptile diversity is most influenced by temperature, whereas the endothermic taxa follow a water-temperature effect (McCain, 2010). Our study is the first to demonstrate the water-temperature effect in a group of montane invertebrates, showing patterns along an altitudinal transect more similar to those found in endothermic than ectothermic vertebrates.

In general, richness of lowland butterflies is often explained by water-energy variables and peaks where physiological stress is lowest (Diniz-Filho et al., 2010). The water-temperature effect implies that species richness on altitude gradients is correlated with productivity, as observed with endothermic vertebrates (McCain, 2010). On our transect, productivity, as established by available moisture and mean annual temperature, is highest at intermediate elevations in the Puna shrub belt in the zone where plant cover and diversity peak (Latorre, 2002), as we show butterfly diversity does as well. A larger-scale analysis of factors governing butterfly species richness in different regions of Chile showed that, in the Northern Puna highlands and Atacama desert ecoregions, the most important predictors for butterfly richness are increases in temperature and elevation (Samaniego and Marquet, 2009).

Previous studies examining insect abundance along mountain ranges with inverse precipitation and temperature gradients have shown similar mid-elevation peaks: ant diversity peaks at mid-elevation in the Mojave desert (U.S.A.) (Sanders, 2003), as do soil micro-arthropods in the winter-precipitation arid zone of Chile (Cepeda-Pizarro, 2004) and butterflies in Israel (Levanoni et al., 2010). However, Fleishman et al. (2000) showed that, in the Great Basin (U.S.A.), butterfly species richness decreased with altitude in one range, but increased in another. In neither case was there a clear relationship with water availability, and the authors concluded that range-specific climate gradients contribute to variation in species richness. In the Salar de Atacama region, Saiz et al. (2000) listed higher abundance, species richness, and Shannon diversity of herbivorous arthropods in pre-Puna and Puna than in Andean steppe and Subnival zones. By contrast, Jerez (2000) found more Coleoptera species in the higher altitude vegetation belts. In another study in this region, bird species richness was shown to increase with altitude, and insect richness to peak at intermediate altitudes (Marquet et al., 1998). Unfortunately, in these studies, confounding of oasis and cordilleran slope sites in the lower vegetation belts and the low number of samples make these results difficult to interpret.

An alternative hypothesis suggests that mid-elevation peaks in species richness are expected in the absence of specific altitude effects on diversity, due to spatial constraints (Grytnes and McCain, 2007). However, this mid-domain effect does not apply to our data because the distribution ranges of species we observed were not abutted by hard boundaries, as the mid-domain effect requires. Indeed, several of the species recorded in this study were also observed at lower altitudes, in the oases around the Salar de Atacama.

DIVISION INTO ENTOMOFAUNAL ZONES

The butterfly fauna seems to be divided into three zones along the transect: a high-altitude zone, dominated by *Palmaris penai*, *Faunula leucoglene*, and *Pierphulia rosea*; a mid-altitude zone dominated by *Madeleinea pelorias* and *Hypsochila sulfurodice*; and a low-altitude zone dominated by *Strymon flavaria* and *Vanessa carye* (Fig. 3). The satyr *Vanessa carye* was the only species to be found at most stations along the transect.

These butterfly-delimited zones correspond approximately to the classic vegetation belts described for northern Chile (Fig. 5): the high-altitude zone (4500–4850 m stations) corresponds to the high Andean steppe and Subnival vegetation belts, the mid-altitude zone (3600–4100 m) corresponds to the Puna shrub belt, and the low-altitude zone (3000–3300 m) corresponds to the pre-Puna shrub belt. Similarly, attempts to divide Chile into entomofaunal regions based on tenebrionid beetles (Peña, 1966) or polyommatine butterflies (Benyamini, 1995) distinguish between the Subnival belt, the Puna belt, and the oasis biome. Benyamini (1995) records *Madeleinea pelorias* and *Strymon flavaria* as characteristic of the Puna belt; our findings suggest that his Puna zone can be further separated into lower and middle altitude belts.

Butterflies are closely linked to plants, and previous work suggests that the altitudinal distribution of a butterfly might depend on that of its larval host plant (Brehm et al., 2003; Hodkinson, 2005; Pyrcz et al., 2009). Altitudinal patterns in butterfly diversity are often similar to those of plants (Hawkins and Porter, 2003), and reflect both the organisms' environmental requirements and the trophic relationships between them.

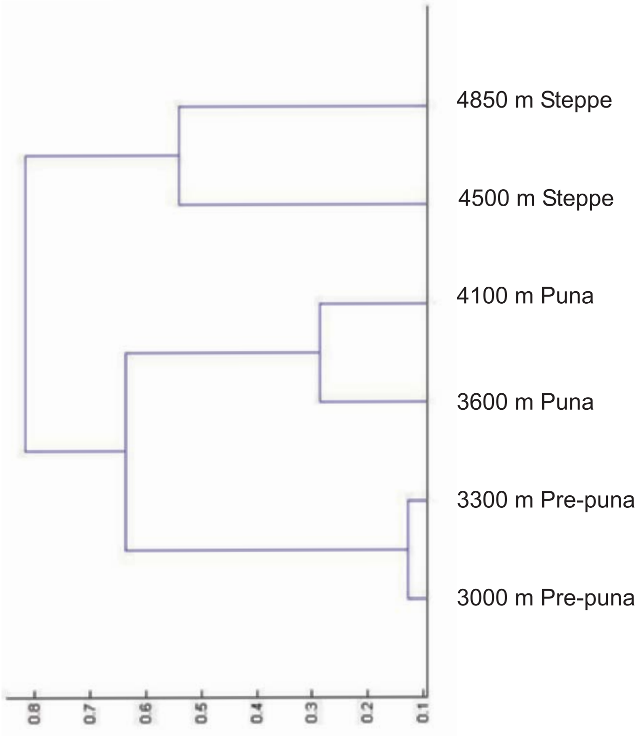

FIGURE 5. Dendrogram of butterfly community similarity among sites. Dendrograms illustrate the results of single linkage cluster analyses based on the Chao-Jaccard abundance-based similarity estimator. Values on the *x*-axis indicate the difference between sites or nodes. The dominant plant community at each site is given at the right.

Phenological Patterns

Most species showed one, sometimes very extended, peak of activity per year, occurring either in spring, mid-, or late summer (Fig. 3). Figure 3 shows that some high-altitude butterflies (e.g. *P. penai* and *F. leucoglene*) were active as adults in the spring when precipitation was just beginning, while others (e.g. *P. rosea*) were seen as adults in mid- to late summer, as the vegetation developed. Low-altitude species were generally seen in mid- to late summer. Summer monsoon precipitation crossing over the Andes begins earlier in the season at higher altitude (Schmidt, 1999). At lower altitudes, plant growth depends mostly on subsurface run-off from precipitation upslope. This earlier availability of moisture at higher altitude might explain why a spring fauna occurs at high but not low altitude.

Gutiérrez and Menéndez (1998) working in northern Spain with a Euro-Siberian climate and no summer dry season, showed that butterflies were present for a shorter and later period at higher altitude. All species found at three or more elevations had later flight periods with increasing altitude, and most showed a shorter flight period. Gutiérrez-Illan et al. (2012) working in the same region further showed that the delay was more pronounced in low-altitude species and earlier season flyers. These patterns were not observed in our study, presumably because the gradient in altitude represented not only changes in temperature, but also in water availability.

Verity (1920), working in the Italian Apennines and Alps, found a more complex relationship between phenology and altitude and divided the butterfly fauna into three elevational types. First, low-altitude species showed shorter flight periods with altitude. In these species, early spring flyers showed delayed flight seasons but later summer species did not; Verity (1920) attributed this difference to longer persistence of spring snow at high elevation. Second, mid-altitude species were constrained by drought at low altitude and showed longer flight periods with increasing elevation. Finally, montane species were only found at high altitude. Figure 4 suggests a similar pattern with the low-altitude *S. flavaria* showing a shorter flight period at higher altitude, and 4 mid- to high-altitude species with the opposite trend. On our transect, butterfly activity in spring is more constrained at lower altitude due to drought, and in late summer is more constrained at higher altitude due to cold. We observe spring activity earlier at high altitude and more late summer activity at low altitude (Fig. 4). Like Verity (1920), we conclude that altitudinal differences in phenology reflect changing environmental conditions in space and time and varying species requirements.

These differences in phenology presumably reflect differences in species lifecycles (Hodkinson, 2005): larvae must be active when host plant foliage is available, but adults can occur at different times of year depending on overwintering strategy (Shapiro, 1975). The larval forms and host plants have been described for some of the species in this study (Courtney and Shapiro, 1986; Shapiro and Courtney, 1986; Benyamini, 1995), but there is no evidence regarding diapause or overwintering strategies. In general, little is known about the ecology and life history for most of these butterflies.

Conclusions

The present study shows that butterfly communities vary strongly with altitude, indeed that the slope between the Salar de Atacama and the altiplano can be divided into three entomofaunal zones based on steep turnover in butterfly species. This variation in butterfly communities supports McCain's (2007) water-temperature hypothesis, showing the mid-altitude peak in diversity predicted for mountains with opposing temperature and precipitation gradients. Mid-altitude is also the zone with highest plant productivity and diversity, and presumably that where physiological stress is least. At the community level, butterfly activity appeared earlier at high altitude, contrary to observations in the temperate zone and presumably due to earlier water availability. The relationship between butterfly phenology and altitude varied among species. Our results suggest that, in arid-region mountains, altitudinal effects on phenology include temperature constraints at the top of the gradient and drought constraints at the bottom, acting in opposite directions. In the Atacama, the absence of a high-altitude snowpack and the summer monsoon precipitation regime implies that temperature constraints act mostly at the end of the season and drought constraints at the beginning. The way these constraints influence individual species' flight period depends on their lifecycle, their larval and adult ecological requirements, and their relationship with host plants.

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