

Title: Changes in butterfly distributions and species assemblages on a Neotropical mountain range in response to global warming and anthropogenic land use

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Abstract

Aim

To assess changes in the elevational distribution of 151 butterfly species over a period of 22 years (1988-2011) and investigate whether these changes are related to regional global warming and land-use change.

Location

Sierra de Juárez, Oaxaca, Mexico.

Methods

Butterflies were surveyed at eight sites spanning elevations ranging from 117 m to 3,000 m in 1988, and the same sites were resurveyed in 2010-2011. Changes in the elevational distribution of species and the structure and composition of species assemblages were compared between surveys. The results were interpreted in the context of land-use and climate change in the region.

Results

Butterfly species had shifted their distributions uphill by approximately 145 m on average. Significantly more species (78) showed an uphill shift in their distributions than a downhill shift (32 species). Species occurring above 1,000 m elevation had shifted their distribution

to an extent that matched the range shift expected under the recorded temperature changes. However, for species occurring below 1,000 m elevation, and for all species combined, uphill range shifts were significantly less than expected based solely on the increase in temperature. Land-use change over the study period was more pronounced at low elevations, and these butterfly assemblages are now dominated by generalist species.

Main Conclusions

Our results represent the first concrete evidence of shifts in elevation distribution of a large Neotropical butterfly community, attributable to increased regional temperatures. At high elevations, land-use change is minimal and climate change appears to be the main driver of changes to distributions and assemblages, and the main conservation threat. However, extensive land-use change has been the main driver of changes to butterfly communities at lower elevations.

Keywords: butterfly assemblages, climate change, elevational gradient, mountain biodiversity, Oaxaca, tropical montane ecosystem.

(A) INTRODUCTION

The effects of global warming on species distributions have been widely documented over the last 20 years. In temperate latitudes, shifts in the latitudinal and elevational distribution of species have been reported for a wide range of taxa (Parmesan, 2006). However, evidence for the effects of global warming on species' distributions in tropical habitats is sparse (but see Pounds *et al.*, 1999; Bustamante *et al.*, 2005; Colwell *et al.*, 2008; Raxworthy *et al.*, 2008; Chen *et al.*, 2009; 2011a; 2011b). This data gap arises mainly because of a paucity of long-term biological and climatic datasets.

Since elevational temperature gradients in tropical regions exert a stronger effect on species' distributions than latitudinal gradients (Colwell *et al.*, 2008), the most likely response of tropical organisms to global warming is an uphill shift in their elevational distributions (Pounds *et al.*, 1999; Bustamante *et al.*, 2005; Colwell *et al.*, 2008; Chen *et al.*, 2009; 2011a). Moreover, it has been suggested that tropical montane endemic species are more susceptible to the effects of global warming than relatively widespread species (Rull & Vegas-Vilarrúbia, 2006; Raxworthy *et al.*, 2008; Chen *et al.*, 2009).

Tropical mountains are characterized by minimal overlap in temperatures at low and high elevations and hence tropical species have evolved within narrow thermal bands, resulting in tight physiological adaptations (Janzen, 1967; Ghalambor *et al.*, 2006; McCain, 2009). As a result, many tropical insects have been shown to occur under conditions very close to their thermal optima (Deutsch *et al.*, 2008), making them very sensitive to temperature changes.

Recent research suggests that the elevational distributions of tropical birds (Forero-Medina *et al.*, 2011; Pounds *et al.*, 1999; Freeman & Freeman, 2014), frogs (Bustamante *et al.*, 2005; Raxworthy *et al.*, 2008), and moths (Chen *et al.*, 2009; 2011a) are shifting, but current research in tropical systems is taxonomically and geographically restricted. If these trends occur more widely among taxa in different parts of the tropics, changes in community structure and disruption of food webs could result in serious reductions in biodiversity, particularly when acting in combination with other drivers of biodiversity change such as habitat loss and degradation. Further research is therefore needed to explore the extent to which temperature changes in tropical regions exert an effect on species' distributions, and how the effects of changes in climate interact with concurrent changes in land use to alter the distributions of species and the structure of ecological assemblages.

In this paper we provide the first empirical evaluation of the effects of recent climate change on the distributions of Neotropical butterflies. We investigate changes in the elevational distributions of butterflies in a Mexican mountain range over a 22-year period, and examine the roles that both regional global warming and anthropogenic land-use changes play in elevational range shifts of these species and associated changes to the composition of species assemblages.

(A) METHODS

(B) Study Area

The study was conducted in the Sierra de Juárez mountain range in northern Oaxaca, Mexico (Fig 1). Below 1,000 m elevation the regional climate corresponds to a warm to

semi-warm humid zone with rains throughout the year. Elevations spanning 1,000 to 2,000 m correspond to a temperate-humid climate with abundant rain in summer (May to October). Elevations above 2,000 m include a temperate humid climate with summer rains (García, 1987). The mean annual temperature at 100 m elevation is *c.* 24.8°C with an estimated lapse rate of 5.2°C per 1,000 m, comparable to other Neotropical elevational gradients (Lieberman *et al.*, 1996). The vegetation zones include evergreen rainforest (100 to 1,400 m elevation), cloud forest (1,400 to 2,250 m), *Quercus* and *Pinus* forests (2,250 to 2,800 m), and *Pinus rudis* Endl., forests with a dense understory of Ericaceae (above 2,800 m) (Rzedowsky & Palacios-Chávez, 1977).

(B) Butterfly Data Collection

Eight sites spanning elevations ranging from 117 m to 3,000 m were surveyed in 1988 (Luis-Martínez *et al.*, 1991) and resurveyed in 2010-2011 using 500 m fixed transect routes (Molina-Martínez *et al.*, 2013). Butterflies were sampled using transect walks and Van Someren-Rydon traps; sampling locations are indicated in Fig. 1. Our sampling periods included the major period of adult butterfly activity during April-October (Luis-Martínez *et al.*, 1991; Vargas-Fernandez *et al.*, 1992; Molina-Martínez *et al.*, 2013).

Consistency of sampling techniques between the time periods was facilitated by A. L.-M., who was involved in both the 1988 and 2010-2011 surveys. In 1988, field sampling was carried out over a 98-day period, while the 2010-2011 field observations spanned 99 days: each site was surveyed on 18 to 24 occasions during May to October 2010 and March to May 2011, for a total of 219 transect-events.

The 2010-2011 resurveys were designed to repeat the same number of recording days at all sites (see Table 1). The 2010-2011 census recorded more individuals than the 1988 census, except for the sites at 600m and 800m elevation, where we recorded fewer individuals than in 1988.

Species richness and abundance for the families Papilionidae, Pieridae and Nymphalidae were recorded. These families are well known taxonomically and have been the subject of intense sampling and identification by us throughout a number of regions in Mexico (e.g. Luis-Martínez *et al.*, 2003; Molina-Martínez *et al.*, 2013).

(C) Temperature data

Reliable long-term temperature data are difficult to obtain in many Neotropical areas. In our study area, historical temperature data are available from three meteorological stations located at 117 m, 1,000 m and 3,200 m elevation for the years 1991, 1992, 1995 and 1996, providing the closest available indication of temperatures corresponding to the 1988 butterfly survey. Because these data were not specific to the sampling sites, we calculated the lapse rate (i.e. the rate at which temperature decreases with increase in altitude) in each year to obtain an estimate of the temperature for each sampling site, i.e. the average temperature value at each site for 1991, 1992, 1995 and 1996. To test whether temperature trends change with elevation, we compared (using ANOVA) temperature variations from the meteorological stations located at 117 m, 1,000 m and 3,200 between historic and current periods, for which actual temperature records were available. For the 2010-2013 time period, temperature data were obtained using data loggers (USB-502, Logicbus ®) in each of the sampling transects across the elevational gradient from June 2010 to May 2013.

Data loggers were located along transects at each of the elevation sites (see Fig. 1). Data loggers were attached to a tree branch, in sites with dense vegetation cover at a height of roughly 2-3 m above ground level. Data loggers were programmed to register temperature and humidity values every hour and data were downloaded every other month.

(D) Land-use Change

In the 22 years since the original survey was conducted, intense land-use change has occurred in the study area, predominantly below 1,000 m elevation. Using Landsat images of the study area, we quantified the total extent of land-use change between 1988 and 2010 across the entire gradient (ca. 76,892 ha). In addition, we quantified the actual extent of land-use change between 1988 and 2010 for each butterfly sampling elevation site using 1,000 m x 1,000 m grid cells (N=8). Ten categories of land-use covers that could potentially be occupied by butterflies were distinguished and the area of each was quantified and compared between time periods for each site (see Fig. 1 and Appendix S3 for site and land-use categories list and details).

Data analysis

(E) Sample completeness

To evaluate if the number of species sampled was representative of the community present at each elevation, we drew individual-based rarefaction curves (Chao & Jost 2012) for each site. Sample completeness estimators were computed using the software iNEXT

(interpolation/extrapolation) available online at <http://chao.stat.nthu.edu.tw/blog/software-download/>. This allowed us to compare butterfly communities while standardising sampling completeness (Chao & Jost 2012). Total species richness was estimated using the abundance-based non-parametric Chao1 estimator (Colwell et al., 2012). Abundance-based estimators have been shown to be less biased than incidence-based estimators for mobile organisms (Brose & Martinez, 2004). In addition, a measure of dominance was calculated using the proportion of individuals for the most common species in each site (Berger-Parker index; Magurran 2004).

(F) Elevational changes

Butterfly abundance data were used to assess changes in the average weighted elevational distribution of each species (Chen *et al.* 2009; 2011a; Forero-Medina *et al.*, 2011). Average weighted elevational distribution was calculated as follows: i) the number of individuals at each elevation was expressed as a proportion of total abundance for all elevations, ii) each elevation was weighted by the proportion of individuals of the species in question at each elevation, and then iii) all such weighted elevations were summed for all elevations to give an average weighted elevation.

The change in average weighted elevation for each species between the two surveys was then calculated in two different ways. First, we used the raw data for all species recorded in both periods ($n = 151$), and for species with abundances equal to or greater than three individuals recorded in total (summed across all sites) in both surveys ($n = 110$). Second, since the 1988 and 2010/2011 surveys recorded different numbers of individuals at some locations, we selected random subsamples of individuals from each survey to generate identical sample sizes (number of individuals) in both surveys for each site. For

example, to generate equal-abundance data sets for the two time periods, we randomly selected a total of 3,969 individuals (the number of individuals recorded for 1988) from the 4,403 individuals recorded in 2010 (see Table 2). In addition, we explored the effects of subsampling both time periods to lesser figures than the smaller sample size using equal-abundance data sets (i.e. 3500, 3000, 2500 and 2000 individuals in each data set; see Table 2 and 3), which allowed us to examine the stability of our results -in regards to the results obtained from raw data for all species. We obtained bootstrap estimates (using R 3.3; R Development Core Team 2014) to estimate 95% confidence intervals of the average weighted elevations for each species, by randomly sampling 2,000 estimates of the change, with replacement, for all species recorded in both periods ($n = 151$), and separately for species where recorded abundances equaled three or more individuals recorded in total (summed among all sites; $n = 110$) in both surveys. We produced 2,000 bootstrap estimates since this figure has been considered adequate to obtain stable estimates of confidence intervals (Efron & Tibshirani 1993). Significant differences for bootstrap estimates of confidence intervals for the average weighted elevations was used as a criterion to categorize species as showing uphill, downhill or no shifts in their elevational distributions in 2010-2011, compared to 1988. We examined the distribution of uphill compared to downhill (or no) distribution trends for the raw data for all species and for random subsamples using sign and T tests. This was done separately for the entire gradient and for sites below and above 1000 m elevation.

Data on the average weighted elevations for all butterfly species were divided into three groups for analysis: (i) data for all species, irrespective of their elevational ranges, (ii) data for species whose average weighted elevation fell below 1,000 m in 1988, and (iii) data for all species with average weighted elevations above 1,000 m in 1988. This

categorization allowed us to separate the possible effects of land-use change (which has been more pronounced at low elevations; see below) from the effects of temperature change.

We divided the temperature records similarly: for both periods, we considered the average temperature for the entire gradient (across all sites), and separately for the sites below or above 1,000 m elevation. Temperature variations from three meteorological stations located at 117 m, 1,000 m and 3,200 m between historic and current periods were examined in detail (see above).

Finally, given the extensive habitat change documented (see below), which could potentially confound the consequences of changes in climate and land-use for butterfly community and distributions; we examined the structure of butterfly species assemblages in two ways.

First, butterfly assemblage composition was compared among elevation sites and between historic and current surveys using ordination by multidimensional scaling (MDS) with the computer package PAST v. 3.01 using 9,999 permutations (Hammer et al. 2001). Two-way PERMANOVA [permutational multivariate analysis of variance (Anderson 2001)] was used to test the independent and the interactive effects between elevation and year periods (1988 vs. 2010) on community structure. The non-parametric PERMANOVA test calculates a pseudo-F statistic (based on permutations) which is comparable to the F statistic from ANOVA and it is not affected by non-normal distributions of data (Anderson 2001). The data were $\log(x + 1)$ transformed for analyses, a procedure which is commonly applied to invertebrate assemblages to weight the importance of occasional large (and patchy) abundance values (Clarke 1993).

Second, we examined the habitat use of each species recorded for the 2010-2011 surveys for sites below and above 1,000 m elevation (shared species between elevation sites were excluded). Based on the habitat description provided by DeVries (1987), and Scott (1986), a habitat use designation was assigned to each species. Butterfly species were classified as (i) occupying unmodified vegetation; (ii) occupying mainly unmodified vegetation but making some use of modified habitats; (iii) occupying modified vegetation; or (iv) occupying disturbed and open habitats (for details see Appendix S1 and S2 in Supporting Information). We compared the abundance changes of species associated with each habitat use designation at sites below and above 1,000 m elevation using ANOVA. A Dunnett test was used for post hoc comparisons, because variance estimates were not homogeneous (SPSS 15.0 software ®).

Finally, we used a generalized linear model to fit a logistic regression equation (using R 3.3; R Development Core Team 2014), with the probability of a significant range shift (p) of a butterfly species as the dependent variable and the habitat-use categories (1,2,3 & 4) and the total abundance recorded for each species between the two censuses as independent variables. Separate logistic regressions were performed for species showing downhill or uphill shifts. In both cases, butterfly species were designated as showing significant range shifts (value 1), or as showing no change (value 0), according to results of bootstrap estimates of elevation shifts. We started with a model that included only a single explanatory variable, and then fitted subsequent models that included both explanatory variables to detect possible confounding effects on range shifts.

(A) RESULTS

(B) Butterfly census

The 1988 survey recorded 4,930 individuals and 221 species, of which 161 were from the family Nymphalidae, 40 Pieridae and 20 Papilionidae. The 2010-2011 survey recorded 5,487 individuals and 178 species, of which 128 species were Nymphalidae, 33 Pieridae, and 18 Papilionidae (Table 1). Elevation changes could be quantified for 151 species (107 Nymphalidae, 30 Pieridae and 14 Papilionidae) recorded in both surveys.

(B) Sampling completeness

Individual-based rarefaction curves for the entire gradient and for each elevation site are shown in Fig. 2. Relative values of sample coverage were higher than 90% for both surveys for each elevation site (Table 1). Extrapolated richness values based on corresponding based-sample sizes revealed that species richness was lower in current (2010-2011) surveys for sites at 117m, 600 m, 800 m, 1,300 m and 1,600 m elevation. An opposite pattern was observed for current surveys above 2,000 m (Table 1). A visual inspection of the rarefaction curves for both periods (Fig. 2) for each elevation site reveals that surveys were relatively complete in terms of documenting total richness (Chao & Jost 2012), and there has been an overall decline in butterfly species richness between the two surveys. The 1988 surveys recorded a higher percentage of singletons and unique species, and higher dominance values (except for sites at 800 m, 1,600 m and 2,000 m elevation, where dominance was comparable for both surveys).

(B) Elevational changes

Table 2 shows the number of butterfly species showing uphill shifts, downhill shifts, or no change in their elevational distribution. For the entire gradient and averaged for all butterfly species ($n = 110$), analyses based on raw data showed that butterflies increased their average weighted elevational distribution by an average of 145 m (Table 3). Uphill shifts were documented for 78 species while 32 species showed downhill trends. Significantly more species exhibited uphill compared to downhill, or no, trends (SIGN TEST: $Z = -4.291$, $P < 0.001$, $N = 110$; Table 2). In addition, significantly more species exhibited uphill compared to downhill, or no, trends, above (SIGN TEST: $Z = -3.714$, $P < 0.001$, $N = 29$), and below 1,000m (SIGN TEST: $Z = -2.667$, $P = 0.008$, $N = 82$). Analyses based on the random sub-sampled data revealed comparable trends (Table 2).

Species with distributions centred below 1,000 m elevation ($n = 81$) shifted significantly their average weighted elevational distribution uphill by an average of 87 m ($P < 0.05$; see Table 3). Uphill shifts were documented for 53 species while 28 species showed downhill trends. Species with distributions centred above 1000 m elevation ($n = 29$) increased significantly their average weighted elevational distribution by an average of 308 m ($P < 0.005$; see Table 3). Of these, 25 species showed uphill trends, compared to four species that showed downhill trends. Random sub-sampled data T tests indicated comparable trends (Table 3).

(B) Temperature trend

Temperature across the entire elevation gradient increased significantly, by an average of 1.3°C, over the two-decade period (Fig 3). Temperatures at sites below and above 1,000 m

elevation had on average increased by 1.8°C, and 0.98°C, respectively. Temperature variations from three meteorological stations between historic and current periods revealed significant temperature increases for sites at 117 m (mean +/- SD for historic and current temperatures = 22.16 +/- 2.4 and 24.56 +/- 2.06, respectively, ANOVA, $F_{1,22} = 6.673$, $P = 0.017$), 1,000 m (mean +/- SD for historic and current temperatures = 17.99 +/- 2.06 and 22.6 +/- 1.92, respectively, ANOVA, $F_{1,22} = 30.55$, $P < 0.001$), and marginal temperature increases at 3,200 m (mean +/- SD for historic and current temperatures = 8.64 +/- 1.57 and 9.94 +/- 1.52, respectively. ANOVA, $F_{1,22} = 4.246$, $P = 0.051$).

(B) Land-Use Change

Land-use intensity in our study area has generated important changes in vegetation cover, particularly below 1,000 m elevation (see Fig 1). The study area covers a total area of 76,892 ha of which 30,127 ha are located below 1,000 m elevation, 32,275 ha are located between 1,001 and 2,000 m elevation, and 14,490 ha are located between 2001 and 3000 m elevation. The most significant change in land use was recorded below 1,000 m elevation, where an increase in agricultural land cover (2,011 ha in 1988 to 9,768 ha in 2010) occurred at the expense of tree fallow and evergreen rainforest (which lost 5,704 ha and 2,730 ha, respectively). Evergreen rainforest also decreased by 2,411 ha through conversion to tree fallow. Land use above 1,000 m did not show major changes from 1988 to 2010 (for details see Appendix S3). These trends remained comparable when we used a finer site-based grid cell (1,000m x 1,000m), showing more pronounced land-use changes over the study period at low elevation sites, and little or no impact at higher elevations (>1,600m elevation; Fig. 4).

(B) Species assemblages

Butterfly community structure and species composition differed significantly between the surveys (PERMANOVA, $F = 2.247$, $P = 0.04$), with each year exhibiting a distinct cluster (Fig. 5). Butterfly assemblages varied significantly between sites below or above 1000 m elevation for 1988 (PERMANOVA, $F = 3.528$, $P = 0.034$), and 2010 surveys ($F = 5.568$, $P = 0.0184$).

The habitat use categories assigned to each species recorded during both surveys are shown in Appendices S1 and S2. Modified or open habitats in sites below and above 1,000 m (Fig. 6) were characterised by a greater fraction of generalist species (i.e. those species using disturbed and open habitats). In sites below 1,000 m, mean species abundance between historic and current surveys differed between those species classified as occupying modified vegetation (ANOVA, $F_{1,68} = 8.848$, $P = 0.004$), and those species classified as occupying disturbed and open habitats (ANOVA, $F_{1,182} = 10.501$, $P = 0.001$). Similarly, the mean species abundance for the current surveys varied among 'habitat use' categories (ANOVA, $F_{3,184} = 12.849$, $P < 0.001$; Fig. 6). In sites above 1,000m, mean species abundance between historic and current surveys differed significantly for species occupying disturbed and open habitats (ANOVA, $F_{1,78} = 5.282$, $P = 0.024$), and those species classified as occupying disturbed and open habitats (ANOVA, $F_{1,20} = 4.467$, $P = 0.04$). The mean species abundance for the current surveys varied among 'habitat use' categories (ANOVA, $F_{3,73} = 8.317$, $P < 0.001$; Fig. 6). Other comparisons yielded non-significant results.

Finally, logistic regression analysis failed to identify that neither an increase of relative abundance nor habitat use categories of a given butterfly species enhanced the probability of showing an uphill or downhill shift (Table 4). Since the minimum adequate

models did not include habitat use categories or abundance or as significant, shifts in species distributions are most plausibly attributed to climate change effects.

(A) DISCUSSION

(B) Elevational shifts in species' distributions

The extent of distribution changes we document here is consistent with those reported in the literature for a variety of taxa, including Lepidoptera from both tropical and temperate regions (e.g. Archaux, 2004; Wilson *et al.*, 2005; Hickling *et al.*, 2006; Lenoir *et al.*, 2008; le Roux & McGeoch, 2008; Chen *et al.*, 2009; 2011a; Forister *et al.*, 2010). In Sierra de Juárez, 65% of the species analyzed showed an uphill trend in their distributions. Butterfly species occurring above 1,000 m showed more marked changes in their elevational distribution compared to species distributed at lower elevations; these higher elevation zones have experienced little land-use change over the past two decades, and we failed to detect significant changes in butterfly community structure between the two surveys at these higher elevations, except for those species occupying disturbed and open habitats which occurred at higher abundance in the recent surveys. Thus, shifts in species distributions at high elevations are most plausibly attributed to climate change and perhaps to colonization events from relatively widespread species. As ectotherms, temperature has a strong effect on Lepidoptera development times (Weiss *et al.*, 1993), fecundity, and time available for flight (Boggs & Murphy, 1997). Some lepidopteran species may have an inherent ability to respond positively to rapid changes or fluctuations in climate (Battisti *et al.*, 2006). This suggests that recorded changes in the elevational distribution of the species reported here could be a direct physiological response to even subtle increases in temperature in the region (Parmesan & Yohe, 2003; Hodkinson, 2005; Chen *et al.*, 2009),

even though the interaction with other organisms may be an important aspect in this process as well.

Species such as *Pterourus pilumnus* Boisduval, 1836, *Nathalis iole* Boisduval, 1836 and *Vanessa virginiensis* (Drury, 1773) were recorded only at the highest elevations (ca. 3,175 m). If projected climate warming over the next two to three decades is realised, these mountain species may experience a complete loss of suitable climate space. Although different individual responses can be expected among the species (i.e. depending on their degree of specialisation and tolerance), the observed shifts in elevational distribution (ranging from 63 m to 307 m) over a period when temperatures increased by approximately 1.3°C suggests that we might see local or regional extinctions in just a few decades for these mountain-affiliated species (see Feely et al., 2013; Moret et al., 2016).

Consistent with previous studies, we found that the rate and extent of elevational distribution changes has not kept pace with those predicted by temperature increase. Previous calculations suggest that in Neotropical systems a temperature increase of 0.52°C might correspond to an increase in elevation of 100 m (Molina-Martínez *et al.*, 2013). Average temperature increases were 1.3°C along the entire gradient, 1.8°C at elevations below 1,000 m, and 0.98°C above 1,000 m; we would therefore expect uphill distribution shifts of approximately 250, 346 and 190 m for species distributed along the entire gradient, below 1,000 m elevation, and above 1,000 m elevation, respectively. Thus, only species with distributions centred above 1,000 m elevation (“high-elevation species”) shifted uphill to the extent required to track temperature shifts. Given that species richness declines with elevation, contrasting responses of “low elevation” and “high elevation” taxa could lead to elevational range shifts calculated for all species being rather low, relative to those predicted by regional warming. Mismatch between the predicted range shifts

associated with the measured temperature increases and the observed distribution shifts may result from nonlinear physiological responses of species to changes in temperature, or because time lags exist between an observed temperature increase and the demographic and distributional response of populations (Lenoir *et al.*, 2010).

(B) Climate change and habitat loss

In our study region, areas of cloud forest and pine forest remained relatively undisturbed above 1,000 m elevation, potentially facilitating the more pronounced range shifts with temperature increases observed for species at high elevations (see Appendix S3). By contrast, land-use change over the study period was more pronounced at low elevations, generating important changes in butterfly assemblages. Our historical and current butterfly censuses at lowland sites demonstrated that a large fraction of the butterfly species assemblage was dominated by generalist species (i.e. species using disturbed and open habitats increased significantly between surveys). We have estimated that 143 (76%) of the species recorded at low elevations are generalists occupying modified or open habitats (see Appendix S1).

The limited distributional shifts of lowland species may be related to land-use change precipitating population declines and local extinctions for species susceptible to environmental changes, limiting their capacity to respond demographically to climate change through elevational range expansions. In any case, land-use changes might also reduce habitat connectivity, which is critical for realising potential range shifts (e.g. Warren *et al.*, 2001). Alternatively, complex topography and microclimatic heterogeneity at lower elevations may generate environmental buffering (Bonebrake & Deutsch, 2012), with areas of relatively stable climatic conditions providing a refuge from climate change and

minimising “forced” range shifts (Scherrer & Körner, 2011). Thus, additive or synergistic effects of climate change and habitat loss may affect species at lower elevations in our study area.

Agrias amydon Kruck, 1931, *Archaeoprepona phaedra* (Goldman & Salvin, 1884), *Fountainea halice* (J. De la Maza & Díaz, 1978), *Memphis philumena* (H. Bates, 1864), *Tithorea harmonia* Godman & Salvin, 1879 and *Napeogenes tolosa* (Hewitson, 1885), (all Nymphalidae) as well as *Itaballia pandiosa* (Reakirt, 1863) (Pieridae), were recorded in 1988, but not during the 2010 – 2011 surveys, indicative of potential population declines or local extinctions as a consequence of increased temperatures, and perhaps exacerbated by habitat loss. However, many of these Neotropical lowland species have extremely localised distributions and low population sizes, with high habitat specificity –a major constraint on their distributions (e.g. León-Cortés et al. 2004). Thus, the relatively small number of historical and current records, and their apparent disappearance from the study area might also reflect their inherent rarity.

Our data suggested an increase of common and relatively widespread species at lowland sites, along with a decrease in rarer and range-restricted species. 76% of species distributed below 1,000 m elevation are species associated with secondary forest and open habitats (DeVries, 1987), which may be symptomatic of a 'lowland biotic attrition' (Colwell et al., 2008). In our study region, as in other environments (Lewis et al., 1998; Warren et al., 2001), land-use change under 1,000 m elevation appears to generate a butterfly community largely composed of generalist species, able to tolerate anthropogenic habitat changes. Nonetheless, our results show that they could be suffering the effects of warming, along with a potential additive effect of warming with habitat modification (i.e. species using modified vegetation were the most likely to show uphill movements). Nonetheless,

such effects might be particularly strong for species with specific habitat requirements, as has been suggested for other tropical (Colwell *et al.*, 2008) and Nearctic (Forister *et al.*, 2010) systems.

Overall, our results represent the first concrete evidence of shifts in elevation distribution of a large Neotropical butterfly community associated with increased regional temperatures. Our historical and current data suggest that, on the one hand, subtle changes in temperature likely influence the high-elevation butterfly community, and on the other, that land-use change in the lowlands appears to generate a butterfly community largely composed of generalist species. Since the ability of butterflies to respond to increases in temperatures depends on the existence of contiguous suitable habitat, the presence of a continuous forested area may be crucial to minimise local extinctions.

At least half of the original area of Mexican cloud forests has been deforested or experienced severe transformations of the understory, notably through the cultivation of 'highland coffee', and plantations under the shade of native tree species (Challenger, 1998). Of concern is that more than half of the area classified as 'forest' corresponds to secondary plant communities (De Jong *et al.*, 1999; Vaca *et al.*, 2011), and that in some Mexican cloud forests, roughly 50% of forest area was lost between 1975 and 2000 (Cayuela *et al.*, 2006). In spite of this, extensive tracts of forest within the Sierra de Juárez, still contain important endemic elements of cloud forests (Almaraz-Almaraz *et al.*, 2013), and these forests are being managed under a community-based conservation approach. The community-based conservation framework developed by local communities might ensure the long-term persistence of continuous habitat that could otherwise mitigate the effects of

increased temperatures and habitat loss by facilitating the establishment and connectivity of new populations in the region.

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(A) SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Check list of butterfly species distributed below 1000 m elevation.

Appendix S2. Check list of butterfly species distributed above 1000 m elevation.

Appendix S3. Description and spatial changes of land-use types in the study area between 1988 and 2010.

BIOSKETCH

Arcángel Molina-Martínez is interested in the study of mechanisms that influence the spatio-temporal distribution of biodiversity along elevational gradients in the context of climate change.

Author contributions: JL L-C, AM-M, HMR and OTL conceived and designed the study; AM-M, JL L-C, ALM, and UC collected the data; AM-M, JL L-C, HMR, OTL, DN, and UC analyzed the data. AM-M, JLL-C, HMR and OTL wrote the manuscript.

Figure legends

Figure 1. Upper: the location of the Sierra de Juárez study area in Southern Mexico, showing the elevation (m) of sampling sites (black circles). Middle: land-use changes within the study gradient between 1988 and 2010 (land-use categories as described in Appendix S3). Bottom: the most significant change in land use was recorded for sites below 1000 m elevation (using 1,000 m x 1,000 m squares), with an increase in agricultural land cover at the expense of tree fallow and evergreen rainforest.

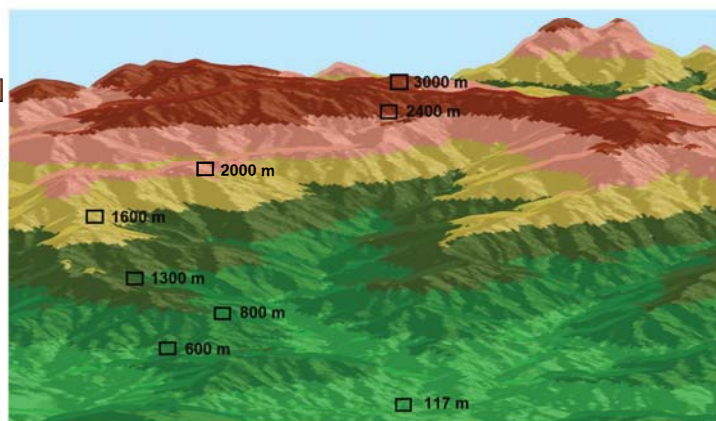
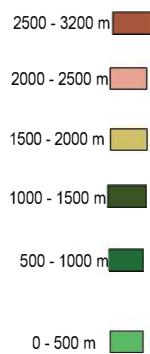
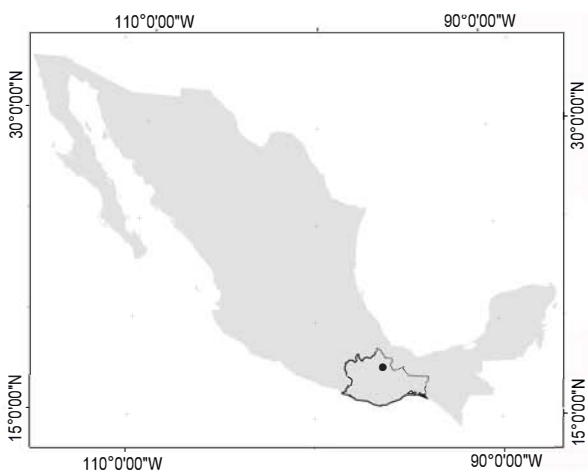
Figure 2. Individual-based rarefaction (solid lines) and extrapolation (dashed lines) curves for each butterfly elevation (m) site and for the entire dataset ('Overall') for 1988 (red curves) and 2010-2011 (gray curves). Reference samples in each comparison are denoted by solid squares or solid circles for the 1988 and 2010-2011 surveys, respectively. All curves have been extrapolated to the corresponding based-sample size (see Table 1 and text, Chao et al. 2014), to show predicted richness for the accumulated number of individuals recorded in each survey. Shaded regions represent 95% confidence intervals based on a 200 bootstrapping replicates.

Figure 3. Annual mean temperature plotted against elevation for 1991-1996 (circles, solid line, slope = -0.0047) and 2010-2013 (squares, dotted line, slope = -0.0051). Symbols represent the location of each sample site in the study area. Site based temperatures for the time period 1991-1996 are calculated according to a lapse rate based on historical temperatures recorded at three meteorological stations in the study area.

Figure 4. Area (hectares) and percentage of land types for 1,000 m x 1,000 m grid cells at each study elevation site in the Sierra de Juárez for years 1988 and 2010. T R F=Tropical Rainforest, T F = Tree Fallow, Agr = Agriculture, C F = Cloud Forest, POF = Pine-Oak Forest, P F = Pine Forest, M = Moorland, R=Riparian, U=Urban.

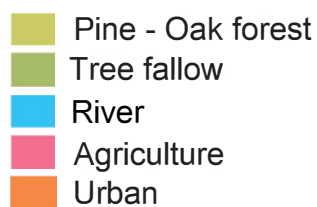
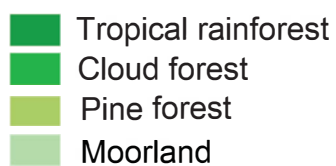
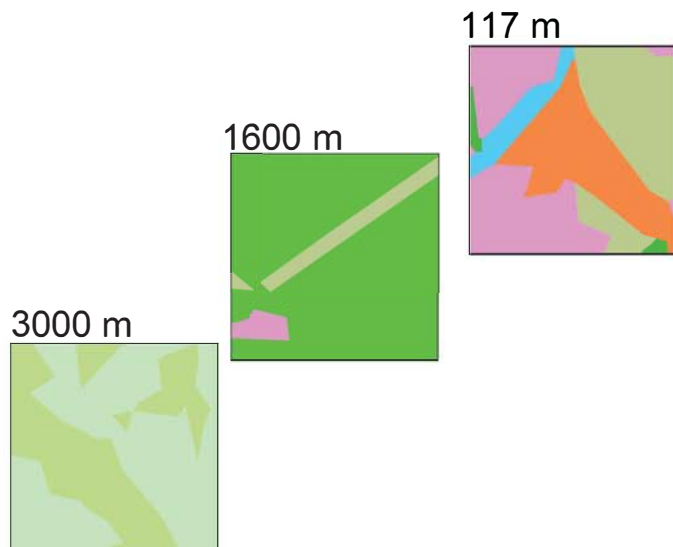
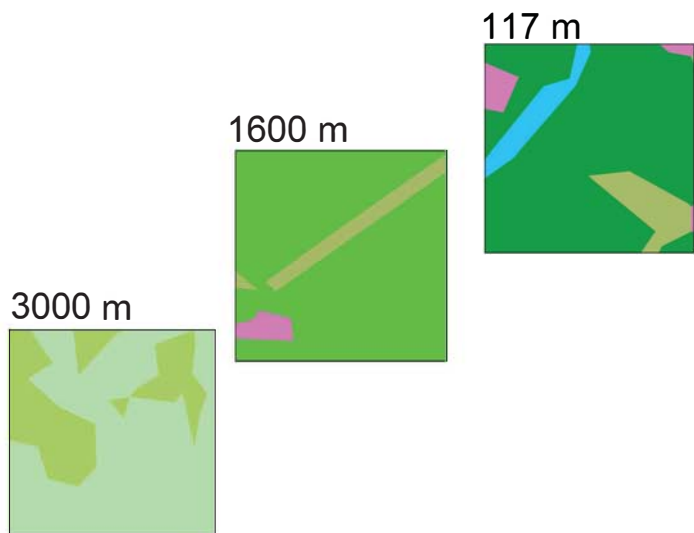
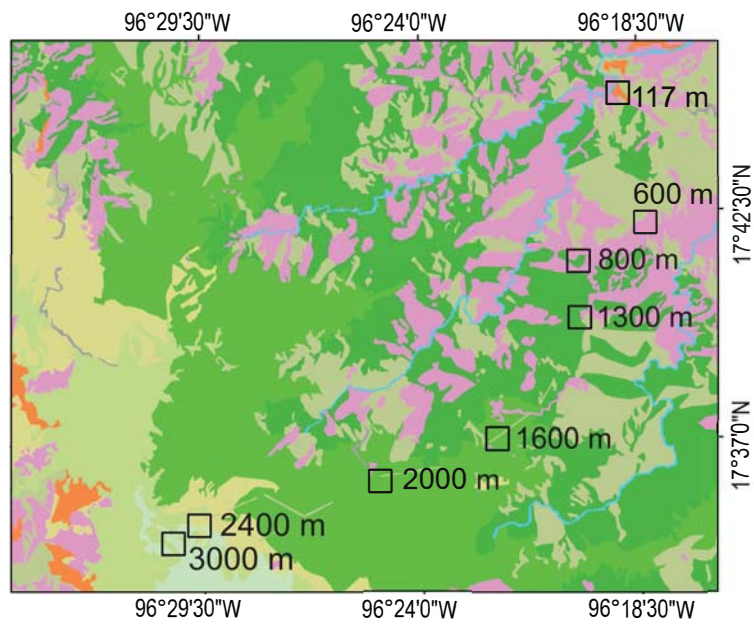
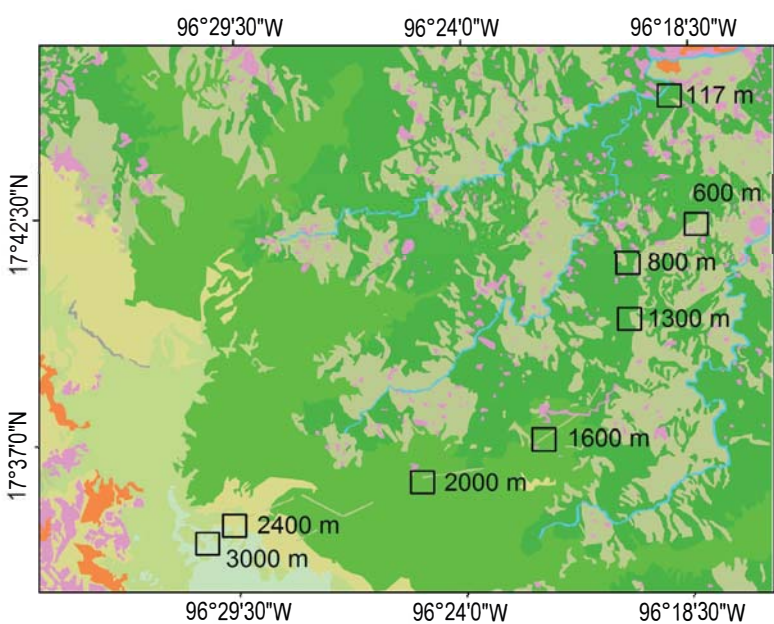
Figure 5. Non-metric multidimensional scaling (NMDS) ordination of butterfly assemblage structure for elevation sites between historic (empty triangles) and current surveys (solid triangles) in the Sierra de Juárez study gradient. Points spaced closer together are more similar in species composition. Bray Curtis, Stress = 0.07316.

Figure 6. Mean values (+/-SE) of species abundance for historic and current surveys of butterflies associated with each habitat-use category, for species distributed (a) below 1,000 m elevation, and above 1,000 m elevation, respectively. Significant differences ($P < 0.05$) within a particular (historic or current) survey (upper case) and within a particular habitat use type (lower case) were marked with different letters.



1988

2010



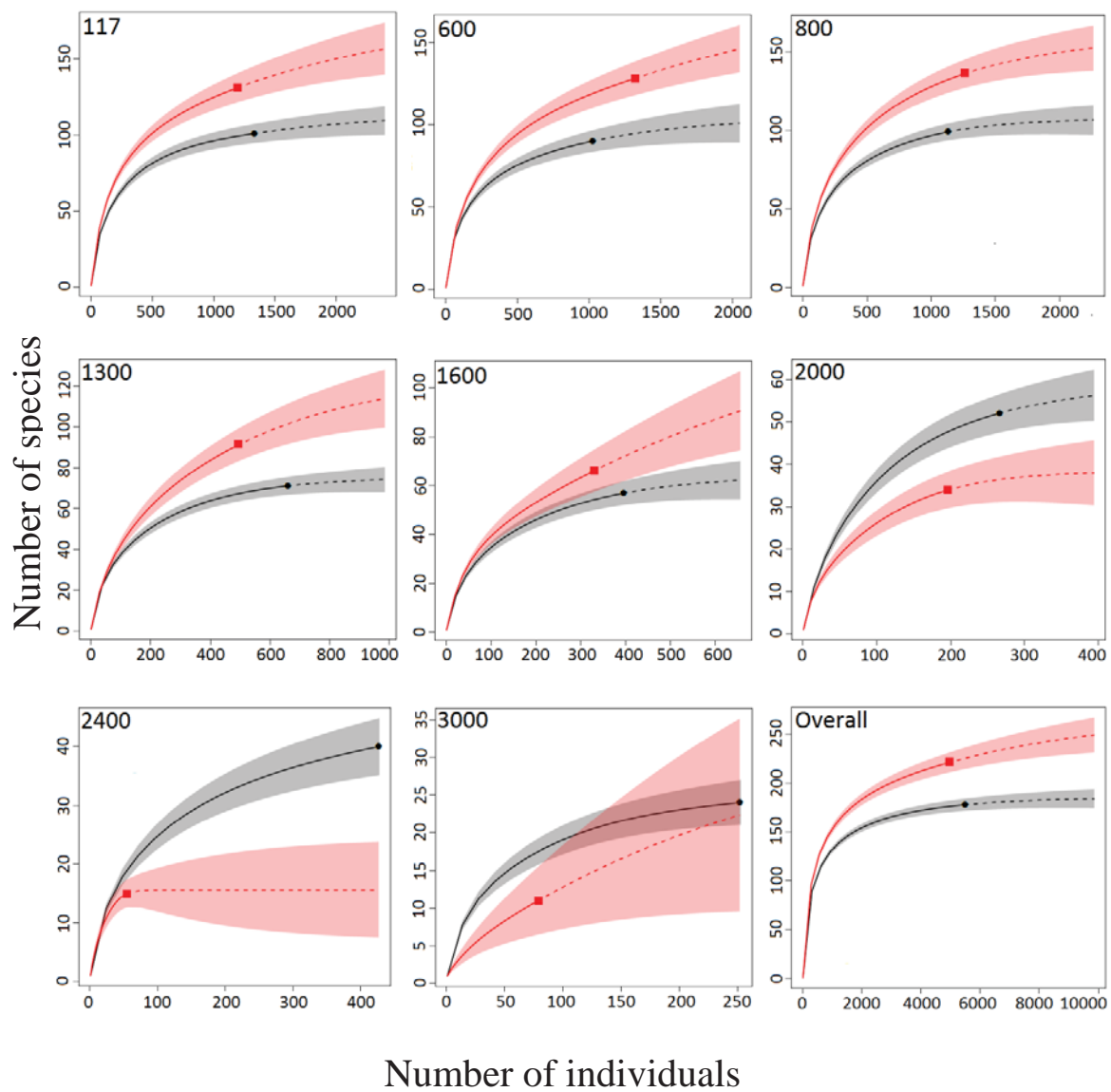
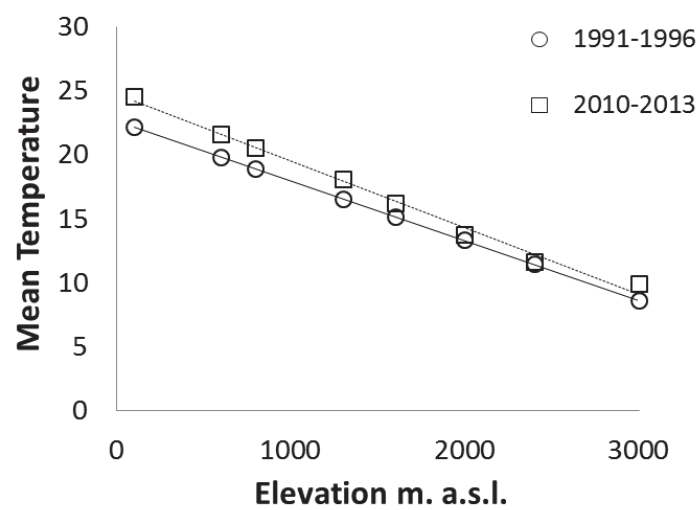


Figure 3



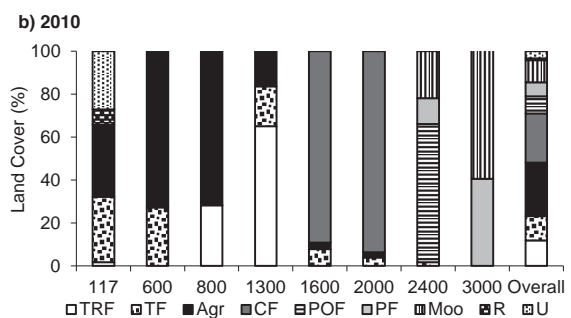
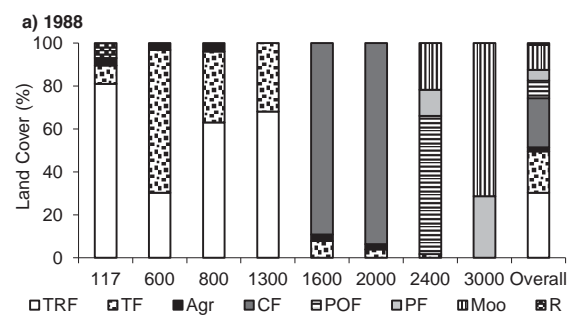
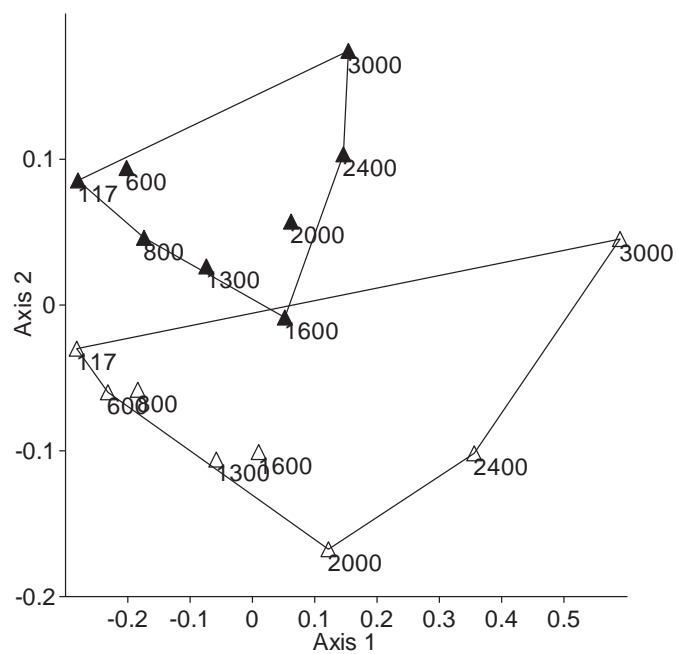


Fig. 5



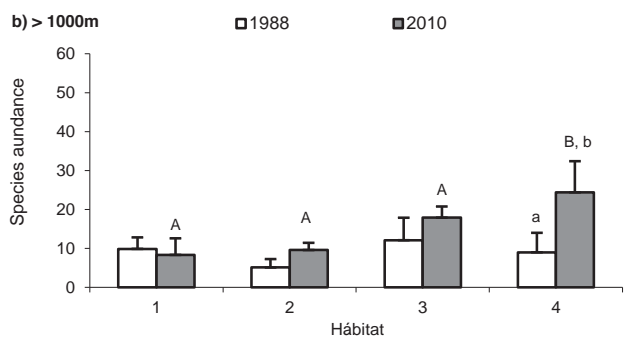
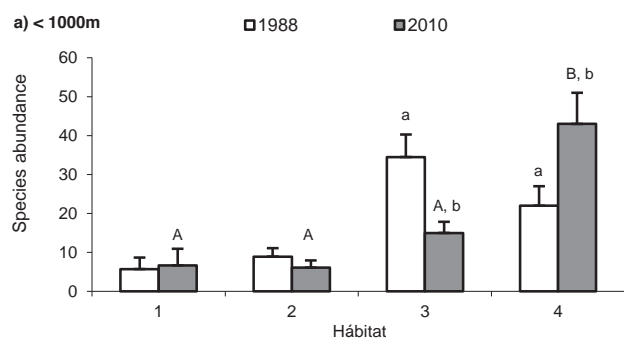


Table 1. Summary of butterfly data recorded in the study elevation sites at Sierra de Juárez, Oaxaca, Mexico

Site*	117	600	800	1300	1600	2000	2400	3000	Overall
No. Individuals	1198/1331	1322/1024	1259/1132	492/659	328/396	197/266	55/427	79/252	4930/5487
No. species	131/101	128/90	136/99	91/71	66/57	34/52	15/40	11/24	221/178
No. singletons ^a (%) ^b	36 (27)/16 (16)	38 (30)/19 (21)	34 (25)/18 (18)	36 (40)/11 (15)	30 (45)/14 (25)	10 (29)/13 (25)	3 (20)/10 (25)	7 (64)/4 (17)	42 (19)/16 (9)
No. doubletons ^c (%) ^b	13 (10)/9 (9)	11 (9)/12 (13)	24 (18)/19 (19)	18 (20)/14 (20)	6 (9)/13 (23)	11 (32)/11 (21)	7 (47)/5 (12)	1 (9)/2 (8)	18 (8)/ 17 (10)
Local uniques ^d (%) ^b	26 (20)/22 (22)	9 (7)/6 (7)	18 (13)/6 (6)	4 (4)/3 (4)	3 (5)/3 (5)	1 (3)/0	0/2 (5)	3 (27)/0	64 (29)/42 (24)
Dominance ^e	0.13/0.08	0.13/0.09	0.14/0.19	0.13/0.09	0.08/0.1	0.18/0.18	0.35/0.25	0.77/0.31	0.1/0.06
Sample coverage (%) ^f	97 (±0.1)/98.8 (±0.1)	97.1 (±0.1)/98.2 (±0.1)	97.3 (±0.1)/98.4 (±0.1)	92.7 (±0.2)/98.3 (±0.1)	90.9 (±0.3)/96.5 (±0.1)	95 (±0.2)/95.1 (±0.2)	95 (±0.5)/97.7 (±0.1)	91.2 (±0.5)/98.4 (±0.1)	99.1 (±0.2)/99.7 (±0.1)
Species richness at equal sample coverage ^{g,s}	91.2 (±4)/61.8 (±3.1)	83.6 (±3.6)/61.9 (±3.1)	86 (±4.6)/66.2 (±3)	82 (±6.9)/52 (±2.7)	66 (±8.6)/44.7 (±3.6)	29.5 (±3.2)/46.1 (±3.8)	14.4 (±2.3)/26.2 (±1.8)	10.4 (±4)/16.7 (±1.7)	123.4 (±2.8)/100.9 (±2.4)
Species richness extrapolated by two ^f	157 (±17)/111 (±10)	157 (±18)/101 (11)	154 (±13)/106 (±11)	114 (±15)/75 (±8)	91 (±16)/63 (±9)	38 (±7)/58 (±8)	16 (±4)/46 (±8)	17 (±8)/26 (±5)	249.2 (±17.3)/184.6 (±9.1)
Chao1 (%) ^h	181 (72)/115 (88)	194 (66)/105 (86)	160 (85)/107 (93)	127 (72)/75 (95)	141 (47)/64 (89)	39 (88)/60 (87)	16 (96)/50 (80)	35 (31)/ 28 (86)	270 (82)/186 (96)

*Collection year 1988/2010

^aNumber of species represented by one specimen

^bPercentage (%) of the total catch.

^cNumber of species represented by two specimens

^dNumber of species recorded on a single site

^eBerger–Parker index

^f(95% confidence intervals)

^gSpecies richness was standardised at the lowest sample coverage (90.9% from site '1600' recorded in 1988)

^hEstimated species richness (% recorded)

Table. 2 Number of butterfly species showing uphill shifts, downhill shifts, or no change in their elevational distribution, based on three alternative methods (see text for details).

		Entire gradient		Below 1000 m a.s.l.		Above 1000 m a.s.l.	
Subsample size		Downhill/Uphill/No change	<i>P</i> value	Downhill/Uphill/No change	<i>P</i> value	Downhill/Uphill/No change	<i>P</i> value
Raw data ^a	Only spp ≥ 3 individuals ^e	32/78/0	***	28/53/0	**	4/25/0	***
RS 1988 and 2010 ^b	Only spp ≥ 3 individuals ^e	31/79/0	***	26/56/0	**	5/23/0	***
	All species ^f	44/97/10	***	38/66/8	**	6/31/2	***
RS 3000 ind. ^c	Only spp ≥ 3 individuals ^e	29/81/0	***	25/57/0	***	4/24/0	***
	All species ^f	44/97/10	***	38/66/8	**	6/31/2	***
RS 2000 ind. ^d	Only spp ≥ 3 individuals ^e	30/80/0	***	26/56/0	**	4/24/0	***
	All species ^f	44/97/10	***	38/66/8	**	6/31/2	***

^aRaw data using 3969 individuals for 1988 and 4403 for 2010

^bRandom subsamples with comparable data sets of 3815 individuals for 1988 and 2010

^cRandom subsamples using only 3000 individuals in each data set

^dRandom subsamples using only 2000 individuals in each data set

^eOnly species with ≥ 3 individuals ($N = 110$ spp) were included

^fAll species ($N = 151$ spp) were included

Sign test significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 3. Results of analyses of butterfly range shifts between the two survey periods, based on three alternative methods of analysis (see text for details).

Subsample size		Entire gradient			Below 1000 m a.s.l.			Above 1000 m a.s.l.		
		Up shift (\pm SE) ^g	T test: T (d.f.)	P value	Up shift (\pm SE) ^g	T test: T (d.f.)	P value	Up shift (\pm SE) ^g	T test: T (d.f.)	P value
Raw data ^a	Only spp \geq 3 individuals ^c	145 (33)	4.37 (109)	***	87 (35)	2.48 (80)	*	308 (72)	4.24 (28)	***
RS 1988 and 2010 ^b	Only spp \geq 3 individuals ^c	149 (32)	4.6 (109)	***	98 (33)	2.9 (81)	**	299 (74)	4.01 (27)	***
	All species ^f	158 (38)	4.13 (150)	***	122 (45)	2.68 (111)	**	264 (69)	3.81 (38)	***
RS 3000 ind. ^c	Only spp \geq 3 individuals ^c	150 (32)	4.61 (109)	***	99 (34)	2.92 (81)	**	300 (75)	4 (27)	***
	All species ^f	159 (38)	4.14 (150)	***	122 (45)	2.68 (111)	**	266 (70)	3.81 (38)	***
RS 2000 ind. ^d	Only spp \geq 3 individuals ^c	149 (32)	4.60 (109)	***	98 (34)	2.89 (81)	**	300 (74)	4.03 (27)	***
	All species ^f	158 (38)	4.11 (150)	***	121 (45)	2.65 (111)	**	265 (69)	3.81 (38)	***

^aRaw data using 3969 individuals for 1988 and 4403 for 2010

^bRandom subsamples with comparable data sets of 3815 individuals for 1988 and 2010

^cRandom subsamples using only 3000 individuals in each data set

^dRandom subsamples using only 2000 individuals in each data set

^eOnly species with \geq 3 individuals (N = 110 spp) were included

^fAll species (N = 151 spp) were included

^gUphill shift in meters

All T tests correspond to one-sample T , $H_0: \mu = 0$ m

T test significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4. The logistic regression model for uphill and downhill shifts of butterfly species in the Sierra de Juárez, Mexico^a. The Z statistic (parameter estimate/SE) tests whether the coefficient is significantly different from 0. The coefficient indicates that as the variable increases (or decreases when it is negative) in value so the likelihood of a butterfly showing uphill or downhill shifts.

Coefficients	Estimate	Std. Error	Z	P
<i>Uphill^c</i>				
(Intercept)	-0.492	0.53	-0.92	0.36
Abundance ^b	0.003	0.003	1.08	0.28
Habitat 3	-0.579	0.65	-0.88	0.38
Habitat 4	-0.660	0.7	-0.94	0.35
Null deviance: 101.7 on 80 degrees of freedom				
Residual deviance: 99.98 on 77 degrees of freedom				
AIC: 107.98				
BIC: 117.56				
<i>Downhill^d</i>				
(Intercept)	-1.335	0.84	-1.59	0.11
Abundance ^b	0.011	0.01	1.2	0.23
Habitat 3	-0.120	1.1	-0.11	0.91
Habitat 4	0.179	1.3	0.14	0.89
Null deviance: 37.4 on 28 degrees of freedom				
Residual deviance: 33.7 on 25 degrees of freedom				
AIC: 41.73				
BIC: 47.2				

^aDue to small sample size, Habitat use categories 1 and 2 were collated for analysis and did not enter the model (see Methods)

^bAbundance: recorded total abundance per species during historic and current butterfly surveys

^cUphill model: species showing uphill shifts = 81 (bootstrap significant shifts, N = 26)

^dDownhill model: species showing downhill shifts = 29 (bootstrap significant shifts, N = 10)

Appendix S1. Butterfly species distributed below 1,000 m elevation. “1988” and “2010” indicate abundance values recorded for each species in each survey period. “T” indicates an uphill or downhill trend (+ or –), respectively. “Change” indicates estimated mean elevational change (m) for butterflies in the study area using raw abundance data; all species that were recorded in both surveys were included. A habitat use designation (“Habitat”) was assigned to each species. Following the habitat description provided by DeVries (1987), and Scott (1986), butterfly species were classified (“HabCat”) as occupying unmodified vegetation (“1”, when no mention was made that butterflies occupy secondary or agricultural habitats), as occupying mainly unmodified vegetation (“2”) but do make some use of modified habitats, but in most cases the latter are used very rarely by these species, and usually only when modified and unmodified habitats are adjacent, as occupying modified vegetation (“3”, when mention was made that they occupy secondary, agricultural, or other human-modified habitats, although most of these species also might occupy unmodified habitats), or as occupying disturbed and open habitats (“4”).

Family	Species	1988	2010	T	Change	Habitat	HabCat
Papilionidae	<i>Battus ingenuus</i> (Dyar, 1907)	4	0			Mature forest	1
	<i>Battus laodamas copanae</i> (Reakirt, 1863)	1	43	+	522	Mature forest	2
	<i>Battus lycidas</i> (Cramer, 1777)	1	0			Mature forest	1
	<i>Batus polydamas polydamas</i> (Linnaeus, 1758)	1	0			Tree fallow	3
	<i>Heraclides anchisiades idaeus</i> (Fabricius, 1793)	0	5			Disturbed and open habitats	3
	<i>Heraclides androgeus epidaureus</i> (Godman & Salvin, 1890)	2	3	+	64	Disturbed and open habitats	3
	<i>Heraclides astyalus pallas</i> (Gray, [1853])	0	4			Disturbed and open habitats	3
	<i>Heraclides cresphontes</i> (Cramer, 1777)	0	74			Disturbed and open habitats	4
	<i>Heraclides rogeri pharnaces</i> (Doubleday, 1846)	1	1	-	681	Disturbed and open habitats	3
	<i>Heraclides thoas autocles</i> Rothschild & Jordan, 1906	3	0			Disturbed and open habitats	4
	<i>Heraclides torquatus tolus</i> (Godman & Salvin, 1890)	1	0			Tree fallow	2
	<i>Mimoides ilus branchus</i> (Doubleday, 1846)	1	0			Tree fallow	4
	<i>Mimoides phaon phaon</i> (Doubleday, 1846)	1	0			Mature forest	3
	<i>Papilio polyxenes asterius</i> (Stoll, 1782)	1	1		0	Tree fallow	3

	<i>Parides erithalion polyzelus</i> (C. Felder & R. Felder, 1865)	2	6	-	205	Mature forest	2
	<i>Parides eurimedes mylotes</i> (H.W. Bates, 1861)	12	6	-	158	Mature forest	2
	<i>Parides iphidamas iphidamas</i> (Fabricius, 1793)	7	5	+	39	Tree fallow	3
	<i>Parides panares panares</i> (Gray, [1853])	12	5	-	413	Mature forest	2
	<i>Parides sesotris zestos</i> (Gray, [1853])	3	4	-	558	Mature forest	2
	<i>Protographium epidaus epidaus</i> (Doubleday, 1846)	1	2		0	Tree fallow	3
	<i>Protographium philolaus philolaus</i> (Boisduval, 1836)	0	1		0	Tree fallow	3
	<i>Pterourus menatius victorinus</i> (Doubleday, 1844)	0	2			Disturbed and open habitats	4
Pieridae	<i>Abaeis nicippe</i> (Cramer, 1779)	31	0			Tree fallow	3
	<i>Anteos clorinde</i> (Godart, [1824])	0	122			Disturbed and open habitats	4
	<i>Anteos maerula</i> (Fabricius, 1775)	2	55	+	542	Disturbed and open habitats	4
	<i>Aphrisa statira statira</i> (Cramer, 1777)	28	63	+	31	Disturbed and open habitats	4
	<i>Archonias brassolis aproximata</i> (Butler, 1873)	1	2	+	195	Tree fallow	3
	<i>Ascia monuste monuste</i> (Linnaeus, 1764)	4	68	+	8	Disturbed and open habitats	4
	<i>Catasticta flisa flisa</i> (Herrich-Schäffer, [1858])	122	0			Tree fallow	3
	<i>Dismorphia amphione isolda</i> Llorente, 1984	16	7	+	138	Mature forest	1
	<i>Dismorphia teucharila fortunata</i> (Lucas, 1854)	16	2	-	109	Mature forest	2
	<i>Enantia albania albania</i> (H.W. Bates, 1864)	2	1		0	Mature forest	1
	<i>Enantia lina marion</i> (Godman & Salvin, 1889)	3	0			Mature forest	1
	<i>Eurema albula celata</i> (R. Felder, 1869)	55	80	+	245	Disturbed and open habitats	4
	<i>Eurema arbela boisduvaliana</i> (C. Felder & R. Felder, 1865)	3	14	+	417	Disturbed and open habitats	4
	<i>Eurema dairia eugenia</i> (Wallengren, 1860)	25	33	+	34	Disturbed and open habitats	4
	<i>Eurema xantochlora xantochlora</i> (Kollar, 1850)	31	0	+	498	Disturbed and open habitats	4
	<i>Ganyra josephina josepha</i> (Salvin & Godman, 1868)	0	5			Disturbed and open habitats	3
	<i>Glutophrissa drusilla tenuis</i> (Lamas, 1981)	3	13	+	311	Disturbed and open habitats	3
	<i>Hesperocharis costarricensis</i> pasion (Reakirt, [1867])	3	0			Tree fallow	3

	<i>Itaballia pandiosa kicaha</i> (Reakirt, 1863)	1	0			Mature forest	1
	<i>Pereute charops charops</i> (Boisduval, 1836)	1	0			Tree fallow	3
	<i>Phoebis agarithe agarithe</i> (Boisduval, 1836)	5	56	-	521	Disturbed and open habitats	4
	<i>Phoebis argante</i> (Brown, 1929)	12	45	+	198	Disturbed and open habitats	4
	<i>Phoebis philea philea</i> (Linnaeus, 1763)	22	91	+	125	Disturbed and open habitats	4
	<i>Phoebis sennae marcellina</i> (Cramer, 1777)	28	143	-	162	Disturbed and open habitats	4
	<i>Pieribalia viardi</i> (Boisduval, 1836)	2	0			Tree fallow	3
	<i>Pyrisitia dina westwoodi</i> (Boisduval, 1836)	1	18		595	Disturbed and open habitats	4
	<i>Pyrisitia nise nelphe</i> (R. Felder, 1869)	73	15	-	404	Disturbed and open habitats	4
	<i>Pyrisitia proterpia</i> (Fabricius, 1775)	27	28	-	319	Disturbed and open habitats	4
Nymphalidae	<i>Actinote guatemalena veraecrucis</i> Jordan, 1913	5	1	-	747	Tree fallow	3
	<i>Adelpha basiloides</i> (H.W. Bates, 1865)	2	1	-	205	Disturbed and open habitats	3
	<i>Adelpha cytherea marcia</i> Fruhstorfer, 1913	2	0			Tree fallow	3
	<i>Adelpha felderi</i> (Boisduval, 1870)	1	0			Tree fallow	3
	<i>Adelpha lycorias melanthe</i> (H.W. Bates, 1864)	0	3			Disturbed and open habitats	4
	<i>Adelpha paraena massilia</i> (C. Felder & R. Felder, 1867)	0	1			Disturbed and open habitats	4
	<i>Adelpha phylaca phylaca</i> (H. Bates, 1866)	2	0			Tree fallow	3
	<i>Adelpha salmoneus salmonides</i> A. Hall, 1938	6	2	+	134	Disturbed and open habitats	4
	<i>Adelpha serpa celerio</i> (H.W. Bates, 1864)	0	12			Disturbed and open habitats	4
	<i>Agraulis vanillae incarnata</i> (Riley, 1926)	6	26	-	376	Disturbed and open habitats	4
	<i>Agrias amydon oaxacata</i> Kruck, 1931	1	0			Mature forest	1
	<i>Anaea aidea</i> (Guérin-Ménéville, [1844])	1	0			Tree fallow	2
	<i>Anartia amathea fatima</i> (Fabricius, 1793)	44	125	-	434	Disturbed and open habitats	4
	<i>Anartia jatrophae luteipicta</i> Fruhstorfer, 1907	23	90	-	280	Disturbed and open habitats	4
	<i>Archaeoprepona demophon centralis</i> (Fruhstorfer, 1905)	4	0			Mature forest	2
	<i>Archaeoprepona demophoon gulina</i> (Fruhstorfer, 1904)	7	0			Mature forest	2

<i>Asterocampa idyja argus</i> (H. Bates, 1864)	2	0			Tree fallow	3
<i>Biblis hyperia aganisa</i> Boisduval, 1836	37	56	+	137	Disturbed and open habitats	4
<i>Caligo oileus</i> (Boisduval, 1870)	8	0			Mature forest	2
<i>Caligo telamonius memnon</i> (C. Felder & R. Felder, 1867)	15	11	+	229	Disturbed and open habitats	3
<i>Caligo uranus</i> Herrich-Schäffer, 1850	0	10			Mature forest	2
<i>Callicore astarte casta</i> (Salvin, 1869)	8	17	+	126	Tree fallow	3
<i>Callicore lyca lyca</i> (Doubleday, [1847])	3	3	-	47	Mature forest	2
<i>Castilia eranites</i> (Hewitson, 1857)	20	26	+	47	Disturbed and open habitats	4
<i>Castilia griseobasalis</i> (Röber, 1913)	0	5			Disturbed and open habitats	4
<i>Castilia myia</i> (Hewitson, [1864])	33	6	+	229	Disturbed and open habitats	4
<i>Catonephele mexicana</i> Jenkins & R.G. Maza, 1985	73	25	+	241	Tree fallow	3
<i>Catonephele numillia esite</i> (R. Felder, 1869)	34	15	-	7	Mature forest	1
<i>Cepheptychia glaucina</i> (H. Bates, 1864)	12	0			Tree fallow	3
<i>Chloreuptychia sericeella</i> (H. Bates, 1864)	73	0			Tree fallow	3
<i>Chlosyne erodyte</i> (H. Bates, 1864)	2	0			Disturbed and open habitats	4
<i>Chlosyne gaudialis gaudialis</i> (H. Bates, 1864)	1	0			Disturbed and open habitats	4
<i>Chlosyne hippodrome hippodrome</i> (Geyer, 1837)	0	15		0	Disturbed and open habitats	4
<i>Chlosyne janais janais</i> (Drury, 1782)	29	7	-	63	Disturbed and open habitats	4
<i>Chlosyne lacinia lacinia</i> (Geyer, 1837)	37	310	-	488	Disturbed and open habitats	4
<i>Chlosyne theona theona</i> Ménétriés, 1855)	10	0			Disturbed and open habitats	4
<i>Cissia labe</i> (Butler, 1870)	96	0			Tree fallow	3
<i>Cissia pompilia</i> (C.Felder & R. Felder, 1867)	159	16			Tree fallow	3
<i>Cissia terrestris</i> (Butler, 1867)	8	135	+	152	Tree fallow	3
<i>Colobura dirce dirce</i> (Linnaeus, 1758)	18	0	+	95	Tree fallow	3
<i>Consul electra electra</i> (Westwood, 1850)	14	2	+	123	Mature forest	2
<i>Consul fabius cecrops</i> (Doubleday, [1849])	18	12	+	159	Mature forest	2

<i>Cyllopsis hedemanni hedemanni</i> R. Felder, 1869	5	0	+	1519	Disturbed and open habitats	4
<i>Danaus eresimus montezuma</i> Talbot, 1943	1	4	-	682	Disturbed and open habitats	3
<i>Danaus gilippus thersippus</i> (H.W. Bates, 1863)	2	7	-	735	Disturbed and open habitats	3
<i>Danaus plexippus plexippus</i> (Linnaeus, 1758)	4	6	-	542	Disturbed and open habitats	3
<i>Diaethria anna anna</i> (Guérin-Ménéville, [1844])	281	0	+	116	Disturbed and open habitats	4
<i>Dione junio huascuma</i> (Reakirt, 1866)	22	16	-	220	Disturbed and open habitats	4
<i>Dircenna klugii</i> (Geyer, 1837)	51	0	+	669	Mature forest	2
<i>Doxocopa pavon theodora</i> (Lucas, 1857)	1	0			Mature forest	2
<i>Dryadula phaetusa</i> (Linnaeus, 1758)	1	0			Disturbed and open habitats	3
<i>Dryas iulia moderata</i> (Riley, 1926)	24	116	-	3	Disturbed and open habitats	4
<i>Dynamine artemisia</i> (Fabricius, 1793)	0	9			Disturbed and open habitats	4
<i>Dynamine postverta mexicana</i> d'Almeida, 1952	45	49	+	137	Disturbed and open habitats	4
<i>Eresia clio clio</i> (Linnaeus, 1758)	23	1	-	108	Tree fallow	3
<i>Eresia phillyra phillyra</i> Hewitson, 1852	75	15	+	2	Tree fallow	3
<i>Eryphanis aesacus</i> (Herrich-Schäffer, 1850)	1	0			Mature forest	1
<i>Eueides aliphaera gracilis</i> Stichel, 1903	18	16	-	248	Tree fallow	3
<i>Eueides isabella eva</i> (Fabricius, 1793)	13	22	+	109	Tree fallow	3
<i>Eueides lineata</i> Salvin & Godman, 1868	6	0	+	279	Tree fallow	3
<i>Eunica monima</i> (Stoll, 1782)	0	4			Disturbed and open habitats	4
<i>Euptoieta hegesia meridiania</i> Stichel, 1938	9	12	-	32	Disturbed and open habitats	3
<i>Euptychia westwoodi</i> Butler, 1867	0	12			Tree fallow	3
<i>Fountainea eurypyle confuse</i> (A. Hall, 1929)	82	11	+	195	Mature forest	2
<i>Fountaynea glycerium glycerium</i> (E. Doubleday, [1849])	42	0			Mature forest	2
<i>Fountaynea halice martinezi</i> (J. De la Maza & Díaz, 1978)	1	0			Mature forest	2
<i>Godyrus nero nero</i> (Hewitson, [1855])	0	2			Mature forest	2
<i>Greta morgane oto</i> (Hewitson, [1855])	11	3	+	321	Tree fallow	3

<i>Hamadryas amphinome mexicana</i> (Lucas, 1853)	9	40	+	102	Tree fallow	3
<i>Hamadryas februa ferentina</i> (Godart, [1824])	12	15	+	420	Tree fallow	3
<i>Hamadryas feronia farinulenta</i> (Fruhstorfer, 1916)	83	34	-	19	Tree fallow	3
<i>Hamadryas glauconome glauconome</i> (H.W. Bates, 1864)	0	21			Tree fallow	3
<i>Hamadryas guatemalena guatemalena</i> (H.W. Bates, 1864)	21	0			Tree fallow	3
<i>Hamadryas iphtime joannae</i> Jenkins, 1983	59	2	-	240	Tree fallow	3
<i>Hamadryas laodamia saurites</i> (Fruhstorfer, 1916)	1	14	+	362	Tree fallow	3
<i>Heliconius charithonia vazquezae</i> W.P. Comstock & F.M. Brown, 1950	13	196	-	147	Disturbed and open habitats	4
<i>Heliconius erato petiverana</i> Doubleday, 1847	4	21	-	151	Tree fallow	3
<i>Heliconius hecalesia octavia</i> H.W. Bates, 1866	4	0			Tree fallow	3
<i>Heliconius hortense</i> Guérin-Méneville, [1844]	65	0	+	639	Tree fallow	3
<i>Heliconius ismenius telchinia</i> Doubleday, 1847	63	28	+	79	Tree fallow	3
<i>Hermeuptychia hermes</i> (Fabricius, 1775)	470	70	+	111	Tree fallow	3
<i>Historis acheronta acheronta</i> (Fabricius, 1775)	1	1	-	683	Mature forest	2
<i>Historis odius dious</i> Lamas, 1995	16	3	-	490	Mature forest	2
<i>Hypoleria lavinia cassotis</i> (H. Bates, 1864)	1	0			Tree fallow	3
<i>Hypothyris lycaste dionaea</i> (Hewitson, 1854)	4	0	+	119	Mature forest	2
<i>Ithomia patilla</i> Hewitson, 1852	75	8	+	591	Tree fallow	3
<i>Junonia coenia coenia</i> Hüber, [1822]	4	0			Disturbed and open habitats	4
<i>Junonia evarete nigrosuffusa</i> Barnes & McDunnough, 1916	0	3			Disturbed and open habitats	4
<i>Laparus doris viridis</i> (Staudinger, 1885)	39	14	+	295	Tree fallow	3
<i>Libytheana carinenta mexicana</i> Michener, 1943	10	5	+	111	Disturbed and open habitats	4
<i>Lycorea halia atergatis</i> Doubleday, [1847]	8	1	-	462	Mature forest	2
<i>Magneuptychia libye</i> (Linnaeus, 1767)	24	9	+	209	Tree fallow	3
<i>Marpesia chiron marius</i> (Cramer, 1779)	17	43	-	340	Tree fallow	3
<i>Marpesia harmonia</i> (Klug, 1836)	11	20	+	227	Tree fallow	3

<i>Marpesia petreus</i> (Cramer, 1776)	1	10	-	329	Tree fallow	3
<i>Mechanitis polymnia lycidice</i> H.W. Bates, 1864	49	9	+	177	Tree fallow	3
<i>Melete lycimnia isandra</i> (Boisduval, 1836)	6	0			Tree fallow	3
<i>Melinaea lilis flavicans</i> C. Hoffmann, 1924	3	0			Tree fallow	3
<i>Memphis moruus boisduvali</i> (W.P. Comstock, 1961)	5	0			Mature forest	2
<i>Memphis philumena xenica</i> (H. Bates, 1864)	13	0			Mature forest	2
<i>Memphis pithyusa pithyusa</i> (R. Felder, 1869)	2	1	+	490	Tree fallow	2
<i>Mestra dorcas amymone</i> (Ménétriés, 1857)	7	2	+	686	Disturbed and open habitats	4
<i>Morpho helenor montezuma</i> Guenée, 1859	20	121	+	130	Tree fallow	3
<i>Morpho theseus oaxacensis</i> Le Moul't & Réal, 1962	0	22			Mature forest	2
<i>Myscelia cyaniris cyaniris</i> Doubleday, [1848]	1	0	+	1176	Tree fallow	3
<i>Myscelia ethusa ethusa</i> (Doyère, [1840])	3	0			Tree fallow	3
<i>Napeogenes tolosa tolosa</i> (Hewitson, 1855)	8	0			Tree fallow	3
<i>Nica flavilla bachiana</i> (R.G. Maza & J. Maza, 1985)	13	0			Tree fallow	3
<i>Oleria victorine paula</i> (Weymer, 1883)	40	0	+	370	Tree fallow	3
<i>Olyras theon</i> H. Bates, 1866	2	0			Mature forest	1
<i>Opsiphanes boisduvallii</i> Doubleday, [1849]	5	2		0	Tree fallow	3
<i>Opsiphanes cassiae mexicana</i> Bristol, 1991	4	0			Mature forest	2
<i>Opsiphanes cassina fabricii</i> (Boisduval, 1870)	4	16	+	296	Tree fallow	3
<i>Opsiphanes tamarindi tamarindi</i> C. Felder & R. Felder, 1861	1	3		0	Tree fallow	3
<i>Pareuptychia metaleuca metaleuca</i> (Boisduval, 1870)	33	31	+	60	Tree fallow	3
<i>Pareuptychia ocirrhoe</i> (Fabricius, 1776)	184	113	+	89	Tree fallow	3
<i>Philaethria diatonica</i> (Fruhstorfer, 1912)	3	28	-	189	Tree fallow	3
<i>Phyciodes graphica vesta</i> (W.H. Edwards, 1869)	1	0	+	2015	Tree fallow	3
<i>Pierella luna rubecula</i> Salvin & Godman, 1868	22	9	-	198	Tree fallow	3
<i>Prepona laertes octavia</i> Fruhstorfer, 1905	6	11	-	27	Mature forest	2

<i>Pteronymia artena artena</i> (Hewitson, [1855])	1	0			Mature forest	2
<i>Pteronymia cotyto</i> (Guérin-Méneville, [1844])	14	0			Mature forest	2
<i>Pyrrhogyra edocla edocla</i> Doubleday, [1848]	2	2		0	Tree fallow	3
<i>Pyrrhogyra otolais otolais</i> H.W. Bates, 1864	3	2		294	Tree fallow	3
<i>Siderone galanthis</i> (Cramer, 1775)	0	1			Tree fallow	3
<i>Siproeta epaphus epaphus</i> (Latreille, [1813])	6	19	-	10	Disturbed and open habitats	4
<i>Siproeta stelenes biplagiata</i> (Fruhstorfer, 19701)	5	0			Disturbed and open habitats	3
<i>Smirna karwinskii</i> Geyer, [1833]	16	0			Tree fallow	3
<i>Taygetis mermeria griseomarginata</i> L. Miller, 1978	3	0			Tree fallow	3
<i>Taygetis uncinata</i> Weymer, 1907	4	0			Tree fallow	3
<i>Taygetis virgilia</i> (Cramer, 1776)	1	0	+	1057	Tree fallow	3
<i>Tegosa anieta luka</i> Higgins, 1981	81	2	+	74	Disturbed and open habitats	4
<i>Tegosa guatemalena</i> (H.W. Bates, 1864)	0	331			Disturbed and open habitats	4
<i>Themenis laothoe</i> (Cramer, 1777)	4	0			Tree fallow	3
<i>Tithorea harmonia hippothous</i> Godman & Salvin, 1879	7	0			Mature forest	2
<i>Vanessa cardui</i> (Linnaeus, 1758)	1	0	+	1910	Tree fallow	3
<i>Yphthimoides renata</i> (Stoll, 1780)	145	0			Tree fallow	3
<i>Zaretis ellops</i> (Ménétriés, 1855)	3	8	+	502	Mature forest	2

Appendix S2. Butterfly species distributed above 1,000 m elevation. “1988” and “2010” indicate abundance values recorded for each species in each survey period. “T” indicates an uphill or downhill trend (+ or –), respectively. “Change” indicates estimated mean elevational change (m) for butterflies in the study area using raw abundance data; all species that were recorded in both surveys were included. A habitat use designation (“Habitat”) was assigned to each species. Following the habitat description provided by DeVries (1987), and Scott (1986), butterfly species were classified ("HabCat") as occupying unmodified vegetation ("1", when no mention was made that butterflies occupy secondary or agricultural habitats), as occupying mainly unmodified vegetation ("2") but do make some use of modified habitats, but in most cases the latter are used very rarely by these species, and usually only when modified and unmodified habitats are adjacent, as occupying modified vegetation ("3", when mention was made that they occupy secondary, agricultural, or other human-modified habitats, although most of these species also might occupy unmodified habitats), or as occupying disturbed and open habitats ("4").

Family	Species	1988	2010	T	Change	Habitat	HabCat
Papilionidae	<i>Eurytides calliste calliste</i> (H. Bates, 1864)	1	11		0	Mature forest	1
	<i>Pterourus esperanza</i> Beutelspacher, 1975	2	11	+	31	Mature forest	1
	<i>Pterourus garamas garamas</i> (Geyer, [1829])	26	69	-	69	Tree fallow	3
	<i>Pterourus pilumnus</i> Boisduval, 1836	0	3			Tree fallow	3
Pieridae	<i>Catasticta flisa flisa</i> (Herrich-Schäffer, [1858])	0	62	+	299	Tree fallow	3
	<i>Catasticta nimbice nimbice</i> (Boisduval, 1836)	1	0			Tree fallow	3
	<i>Catasticta teutila flavifasciata</i> Beutelspacher, 1986	21	12	+	520	Tree fallow	3
	<i>Dismorphia eunoe eunoe</i> (Doubleday, 1844)	2	0			Mature forest	1
	<i>Enantia jethys</i> (Boisduval, 1836)	19	5	+	276	Mature forest	2
	<i>Eurema mexicana mexicana</i> (Boisduval, 1836)	7	69	+	209	Disturbed and open habitats	4
	<i>Eurema salome jamapa</i> (Reakirt, 1866)	56	91	-	165	Disturbed and open habitats	4
	<i>Eurema xantochlora xantochlora</i> (Kollar, 1850)	0	18			Disturbed and open habitats	4
	<i>Hesperocharis graphites avivolans</i> (Butler, 1865)	5	30	-	223	Tree fallow	3
	<i>Leptophobia aripa elodia</i> (Boisduval, 1836)	50	95	+	165	Disturbed and open habitats	4

	<i>Lieinix nemesis atthis</i> (Doubleday, 1842)	13	7	+	536	Mature forest	2
	<i>Nathalis iole</i> Boisduval, 1836	8	108	+	270	Disturbed and open habitats	4
	<i>Phoebis neocypris virgo</i> (Butler, 1870)	11	12	+	34	Disturbed and open habitats	4
	<i>Zerene cesonia cesonia</i> (Stoll, 1790)	8	6	+	224	Disturbed and open habitats	4
Nymphalidae	<i>Adelpha donysa donysa</i> (Hewitson, 1847)	11	5	-	316	Tree fallow	3
	<i>Adelpha iphichus iphichus</i> (Linnaeus, 1758)	1	0			Tree fallow	3
	<i>Adelpha leuceria leuceria</i> (H. Druce, 1874)	47	0			Mature forest	3
	<i>Adelpha leucerioides</i> Beutelspacher, 1975	0	40			Tree fallow	3
	<i>Altinote ozomene nox</i> (H.W. Bates, 1864)	63	5	+	84	Disturbed and open habitats	3
	<i>Anetia thirza thirza</i> Geyer, [1833]	6	14	+	490	Mature forest	2
	<i>Archeoprepona phaedra</i> (Goldman & Salvin, 1884)	11	0			Mature forest	2
	<i>Castilia chinantlensis</i> (R. F. De la Maza, 1978)	4	0			Mature forest	1
	<i>Cissia pseudoconfusa</i> Singer, DeVries & Ehrlich, 1983	0	2			Disturbed and open habitats	3
	<i>Colobura dirce dirce</i> (Linnaeus, 1758)	0	4			Tree fallow	3
	<i>Cyllopsis hedemanni hedemanni</i> R. Felder, 1869	0	1			Disturbed and open habitats	3
	<i>Cyllopsis suivalenoides</i> L.D. Miller, 1974	0	8			Tree fallow	3
	<i>Cyllopsis suivalens escalantei</i> L.D. Miller, 1974	63	147	-	238	Tree fallow	3
	<i>Diaethria anna anna</i> (Guérin-Ménéville, [1844])	0	209			Disturbed and open habitats	4
	<i>Diaetria pandama</i> (Doubleday, [1848])	13	0			Tree fallow	3
	<i>Dione moneta poeyii</i> Butler, 1873	28	94	+	88	Disturbed and open habitats	4
	<i>Dircenna jemina</i> (Geyer, 1837)	21	0			Mature forest	2
	<i>Dircenna klugii</i> (Geyer, 1837)	0	4			Tree fallow	3
	<i>Doxocopa laurentia cherubina</i> (C.Felder & R. Felder, 1867)	4	0			Mature forest	2
	<i>Epiphile adrasta adrasta</i> Hewitson, 1861	1	6	-	12	Tree fallow	3
	<i>Epiphile hermosa</i> J. De la Maza & Díaz, 1978	4	0			Mature forest	1
	<i>Epiphile iblis plutonia</i> H.W. Bates, 1864	5	3	+	507	Tree fallow	3

<i>Episcada salvinia salvinia</i> (H.W. Bates, 1864)	11	16	+	71	Mature forest	2
<i>Eueides lineata</i> Salvin & Godman, 1868	0	82			Tree fallow	3
<i>Greta annette annette</i> (Guérin-Méneville, [1844])	21	4	+	402	Mature forest	2
<i>Gyrocheilus patrobas patrobas</i> (Hewitson, 1862)	1	0			Mature forest	2
<i>Hamadryas fornax fornacalia</i> (Fruhstorfer, 1907)	15	0			Tree fallow	3
<i>Hamadryas guatemalena guatemalena</i> (H.W. Bates, 1864)	0	3			Tree fallow	3
<i>Heliconius hortense</i> Guérin-Méneville, [1844]	0	47			Tree fallow	3
<i>Hypanartia dione disjuncta</i> Willmott, J. Hall y Lamas, 2001	2	24	+	228	Tree fallow	3
<i>Hypanartia godmanii</i> (H.W. Bates, 1864)	21	6	+	123	Mature forest	2
<i>Hypanartia lethe</i> (Fabricius, 1793)	27	5	+	119	Disturbed and open habitats	4
<i>Hypanartia trimaculata autumnata</i> Willmott, J. Hall & Lamas, 2001	9	13	-	502	Tree fallow	3
<i>Hypothyris lycaste dionaea</i> (Hewitson, 1854)	0	2			Mature forest	2
<i>Ithomia leila</i> Hewitson, 1852	36	30	-	66	Tree fallow	3
<i>Marpesia corita corita</i> (Westwood, 1850)	13	89	+	257	Mature forest	2
<i>Marpesia zerynthia dentigera</i> (Fruhstorfer, 1907)	0	1			Tree fallow	3
<i>Memphis proserpina proserpina</i> (Salvin, 1869)	11	2	+	159	Mature forest	2
<i>Morpho polyphemus luna</i> Butler, 1869	1	48	-	386	Tree fallow	3
<i>Morpho theseus oaxacensis</i> Le Moult & Réal, 1962	5	0	-	408	Mature forest	2
<i>Myscelia cyaniris cyaniris</i> Doubleday, [1848]	0	1			Tree fallow	3
<i>Nymphalis antiopa antiopa</i> (Linnaeus, 1758)	8	10	-	6	Mature forest	2
<i>Oleria victorine paula</i> (Weymer, 1883)	0	9			Mature forest	2
<i>Oleria zea zea</i> (Hewitson, [1855])	1	3	+	294	Mature forest	2
<i>Oxeoschistus tauropolis tauropolis</i> (Westwood, [1850])	104	99	+	72	Tree fallow	3
<i>Paramacera chinanteca</i> L.D. Miller, 1972	12	2		0	Mature forest	2
<i>Paramacera xicaque xicaque</i> (Reakirt, [1867])	64	0			Mature forest	1
<i>Pedaliodes circumducta</i> Thieme, 1905	122	121	-	86	Tree fallow	3

<i>Phyciodes graphica vesta</i> (W.H. Edwards, 1869)	0	16			Tree fallow	3
<i>Polygonia g-argenteum</i> (Doubleday, 1848)	0	7			Tree fallow	3
<i>Pteronymia simplex fenochioi</i> Lamas, 1978	0	1			Tree fallow	3
<i>Satyrotaygetis satyrina</i> (H. Bates, 1865)	6	0			Tree fallow	3
<i>Siderone syntycha syntycha</i> Hewitson, [1854]	2	0			Mature forest	2
<i>Smyrna blomfildia datis</i> Fruhstorfer, 1908	74	70	+	79	Disturbed and open habitats	4
<i>Taygetis virgilia</i> (Cramer, 1776)	0	4			Tree fallow	3
<i>Vanessa atalanta rubria</i> (Fruhstorfer, 1909)	1	0			Tree fallow	3
<i>Vanessa cardui</i> (Linnaeus, 1758)	0	4			Tree fallow	3
<i>Vanessa virginiensis</i> (Drury, 1773)	1	66	+	841	Disturbed and open habitats	3
<i>Zaretis callidryas</i> (R. Felder, 1869)	1	0			Mature forest	2

Appendix S3. Description and spatial changes of land-use types in the study area between 1988 and 2010.

The study area includes a mixture of land-use types that have been recognized on the basis of physiognomic characteristics of the vegetation and land management. Land-use features are based on descriptions by Rzedowsky & Palacios-Chavez (1977), with the exception of “Moorland” which followed Miranda & Hernandez-X (1963).

Agriculture: Annual crops, mainly *Zea maiz* and *Phaseolus* spp. crops.

Urban: Areas where natural and semi-natural vegetation has been almost entirely replaced. Gardens or small plots (“parcelas” in Spanish) retain some native tree elements, but at very low densities.

Tree Fallow: Secondary forest of approximately 8-12 years old, with a defined tree canopy of 3-5 m in height. The diameters of the trees exceed 5 cm. This habitat is dominated by fast-growing secondary tree species.

Tropical rainforest: Distributed up to 1,400 m elevation, including species such as *Terminalia amazonica* and *Vochysia hondurensis*, and representatives of the genera *Lonchocarpus*, *Laplacea*, *Ternstroemia* and the Lauraceae family. Tree ferns are also common.

Cloud forests: Distributed from 1,000 to 2,250 m elevation. Common tree species belong to the genera *Ilex*, *Podocarpus*, *Alchornea*, *Engelhardia*, *Quercus*, *Clethra*, *Clusia*, *Oreopanax* and *Persea*.

Pine – Oak forest: Primarily distributed from 2,250 to 2,800 m elevation, and mainly dominated by species from the genera *Pinus* and *Quercus*.

Pine forest: Located above 2,800 m elevation dominated by *Pinus rudis* with an understory composed mainly by members of the family Ericaceae.

Moorland: Area consisting of small plants growing to a few centimeters in height, and mainly comprising grasses (Poaceae) of the genera *Muhlenbergia*, *Trisetum*, *Calamagrostis*, *Poa* and *Agrostis*.

Land-use modifications (ha) estimated over a 22 year-period in the study gradient.
‘Change’ shows the percentage of increase (+), decrease (-), or no change (0), in area cover for each of the land use types.

100 - 1000 m a.s.l. (30127 Has)			
	1988	2010	Change
Agriculture	2011 (6.7)	9767 (32.4)	+ 386
Cloud Forest	55 (0.2)	55 (0.2)	0
River	774 (2.6)	774 (2.6)	0
Roads	0 (0)	58.5 (0.2)	+
Tree fallow	13217 (43.9)	9293 (30.8)	- 30
Tropical rainforest	13968 (46.4)	10024 (33.3)	- 28
Urban	101 (0.3)	154.3 (0.5)	+ 53

1001 - 2000 m a.s.l. (32275 Has)			
	1988	2010	Change
Agriculture	890 (2.8)	2120 (6.6)	+ 138
Cloud Forest	14620 (45.3)	14213 (44)	- 3
Pine Forest	179 (0.6)	160 (0.5)	- 11
Pine – Oak Forest	2547 (7.9)	2143 (6.6)	- 16
River	26 (0.07)	26 (0.07)	0
Road	0 (0)	88 (0.3)	+
Tree fallow	4649 (14.4)	4208 (13)	- 9
Tropical rainforest	9073 (28.1)	8995 (27.9)	-1
Urban	292 (0.9)	323 (1)	+ 11

2001 - 3000 m a.s.l. (14490 Has)			
	1988	2010	Change
Agriculture	367 (2.5)	564 (3.9)	+54
Cloud forest	4695 (32.4)	4677 (32.3)	-0.04
Moorland	1151 (8)	1017 (7)	-12
Pine – Oak Forest	2952 (20.4)	2635 (18.2)	-11
Pine Forest	4844 (33.4)	4943 (34.1)	+2
Road	49 (0.3)	62 (0.4)	+25
Tree fallow	110 (0.8)	249 (1.7)	+126
Urban	321 (2.2)	343 (2.4)	7