

# El Niño and dry season rainfall influence hostplant phenology and an annual butterfly migration from Neotropical wet to dry forests

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## Abstract

We censused butterflies flying across the Panama Canal at Barro Colorado Island (BCI) for 16 years and butterfly hostplants for 8 years to address the question: What environmental factors influence the timing and magnitude of migrating *Aphrissa statira* butterflies? The peak migration date was earlier when the wet season began earlier and when soil moisture content in the dry season preceding the migration was higher. The peak migration date was also positively associated with peak leaf flushing of one hostplant (*Callichlamys latifolia*) but not another (*Xylophragma seemannianum*). The quantity of migrants was correlated with the El Niño Southern Oscillation, which influenced April soil moisture on BCI and total rainfall in the dry season. Both hostplant species responded to El Niño with greater leaf flushing, and the number of adults deriving from or laying eggs on those new leaves was greatest during El Niño years. The year 1993 was exceptional in that the number of butterflies migrating was lower than predicted by the El Niño event, yet the dry season was unusually wet for an El Niño year as well. Thus, dry season rainfall appears to be a primary driver of larval food production and population outbreaks for *A. statira*. Understanding how global climate cycles and local weather influence tropical insect migrations improves the predictability of ecological effects of climate change.

**Keywords:** climate change, El Niño, ENSO, insect flight, insect migration, migratory behavior, resource limitation, tropical rainforest

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## Introduction

Butterfly flight activity has provided important evidence of global climate change (Parmesan, 2006). Climate is a primary factor driving the advance of the first flight of

butterflies in central California (Forister & Shapiro, 2003) and butterfly migrations to the British Isles (Sparks *et al.*, 2005). Climate change is likely to impact tropical biota, as well; and yet, we know practically nothing about the environmental factors driving the long-distance migration of tropical butterflies. This in part is due to the lack of long-term data sets on migrating species in tropical climates (e.g., Haber & Stevenson, 2004).

The roles of biotic and abiotic factors in regulating insect populations are often nonadditively complex. El Niño may be an exception. The global climate cycle characterized as the El Niño Southern Oscillation (ENSO) influences global patterns of primary productivity (Behrenfeld *et al.*, 2001; Stenseth *et al.*, 2002; Holmgren *et al.*, 2006; McPhaden *et al.*, 2006). For example, a warm

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tropical Pacific Ocean surface is associated with increased rainfall in deserts and tropical seasonally dry forests worldwide, resulting in seed germination and plant growth. The effects of increased primary productivity cascade upward into higher trophic levels resulting in periodic outbreaks of herbivorous species (Jaksic, 2001; Holmgren *et al.*, 2006). A number of researchers have hypothesized a link between ENSO, primary productivity, and insect migrations in deserts and tropical seasonally dry forests (see Vandenbosch, 2003). Here, we designate this link between ENSO and insect migrations: the El Niño Migration Hypothesis.

In many tropical wet forests, reduced cloud cover and rainfall and greater solar radiation and temperature are associated with El Niño years (Kiladis & Diaz, 1989). For example on Barro Colorado Island (BCI) in central Panama, Wright & Calderón (2006) found an increase in solar radiation, higher temperatures and a reduction in precipitation during El Niño events, and the opposite effects during La Niña events. Plants appear to respond favorably to increased sunlight and higher temperatures in El Niño years. Although limited in scope, annual tree ring data from central Panama indicate that El Niño events may enhance tree growth (see discussion in Wright & Calderón, 2006). Enhanced plant productivity with El Niño is also observed in measures of reproduction: flower and seed production, although extreme El Niño events may be detrimental to reproduction (Wright & Calderón, 2006). Given this response in productivity, the El Niño Migration Hypothesis may also apply to tropical wet forests.

For 16 years near BCI, we have censused migratory butterflies flying over the Panama Canal at a point in a migratory flyway from the Atlantic (Caribbean) coast to the Pacific coast of the Republic of Panama (Srygley *et al.*, 1996). The butterfly migrations across the isthmus differ from those frequently studied in which insects move away from dry or cold environments (e.g., Larsen, 1976; Brower, 1995; Haber & Stevenson, 2004). Instead, these Neotropical migrations occur near the beginning of the wet season. Seasonal insect migrations are often resource based with spatial and temporal distribution of food supply being the main selective force governing the migratory phenology, rate and direction (e.g., Rainey, 1951; Southwood, 1977; Van Schaik *et al.*, 1993; Loxdale & Lushai, 1999; Dingle & Drake, 2007). Tropical butterfly migrations may follow a gradient of environmental productivity, which in turn is governed by the spatio-temporal distribution of rainfall. In this paper, we address the question: What environmental factors determine the timing and magnitude of migrants crossing the Panama Canal? We evaluate the effect of the ENSO climate cycle on hostplant phenology and a butterfly migration in a Neotropical wet forest.

## Materials and methods

### *Study organisms and study site*

Annually from mid-May to mid-July, *Aphrissa statira* Cramer (Pieridae) migrates directionally across the Panama Canal near BCI (9°10'N, 79°51'W), a nature reserve and biological field station administered by the Smithsonian Tropical Research Institute (STRI). The migratory flyway extends from the Atlantic coastal wet forest to the Pacific coastal dry forest, and the predominant migratory direction at this time of year is south-southwest (Srygley *et al.*, 1996; Oliveira *et al.*, 1998). *A. statira* maintain their migratory direction with a time-compensated sun compass and possess sophisticated mechanisms to maintain their course and reduce the energetic cost while migrating (reviewed in Srygley & Dudley, 2008). As adults, *A. statira* feed on flower nectar, and female *A. statira* lay eggs on lianas in the family Bignoniaceae, including *Callichlamys latifolia* (Rich.) K. Schum. and *Xylophragma seemannianum* (Kuntze) Sandwith. The latter is a new hostplant record (R. B. Srygley & R. Aizprúa, unpublished data). Both hostplant species range from Mexico to Brazil (Flora of the Venezuelan Guayana online at <http://www.mobot.org>).

The isthmus of Panama is characterized by two coastal lowlands separated by a central mountain range stretching east-west along the length of the country. This range falls to near sea level (ca. 200 m) where the migratory flyway occurs in the region of the Panama Canal. Annual rainfall declines from the Atlantic to Pacific coasts. On average, Fort Sherman on the Atlantic coast receives 3020 mm of rain per year, BCI receives 2620 mm, Gamboa in central Panama receives 2230 mm, and Panama City on the Pacific coast receives 1850 mm. Across the isthmus, a distinct dry season, during which rainfall is only one-tenth the annual precipitation (300 mm on the Atlantic and Gamboa, 285 mm on BCI, and 140 mm in Panama City), occurs from mid-December through the end of April. The rainfall gradient influences the proportion of evergreen vs. deciduous trees in the forests across the isthmus.

Our working hypothesis is that the southwesterly directional migration is a result of loss of larval resources in the evergreen Atlantic coastal forest due to overcast skies in the wet season (i.e., light limitation hypothesis, Van Schaik *et al.*, 1993). The deciduous forest of the Pacific coast provides a suitable destination because new growth begins with the onset of wet season and continues to provide a predictable larval resource due to the greater availability of sunlight (Srygley & Oliveira, 2001). Interestingly, *Aphrissa* butterflies migrate northeasterly in September–October toward the evergreen forest before the end of the wet season in December. This behavior may have evolved

due to a seasonal reduction in new leaf production in the deciduous forest as dry season approaches and leaf-flushing events in the wet forest during short dry periods in September–October. Furthermore, the wet forest provides a humid refuge to maintain the population during the dry season (Srygley, 2001). Because of logistic difficulties, we lack hostplant data for *A. statira* at the origin and destination coastal sites, but we present hostplant data from the isthmus to associate leaf-flushing phenology with global and local climate.

#### Counts of migratory butterflies

During each migratory season, we censused the number of butterflies that flew across two 300 m transects over Lake Gatún (an artificial lake flooded in 1914 to form a large part of the Panama Canal). We conducted each census from a boat tied to a stump (9°10.622'N, 79°49.873'W) at the southwest apex of the two transects. Looking north for 1 min between stump and the western promontory of Buena Vista Peninsula (9°10.709'N, 79°50.001'W), a person recorded the species of butterflies

that crossed the transect, the number of each species flying west, and the number flying east. Looking east for 1 min between stump and a southern promontory of Buena Vista Peninsula (9°10.714'N, 79°50.727'W), a person recorded the species of butterflies crossing the transect, the number of each species flying south, and the number flying north. Following these counts, we collected environmental data, including air temperature, wind speed and direction, the sun's visibility, and the proportion of sky covered by clouds. Then we counted the number of butterflies a second time for each transect. An entire census required approximately 5 min when two persons were in the boat and a couple of minutes longer if only one person collected data.

In this paper, we focus on the greatest migratory activity of *Aphrissa* butterflies over the course of the migratory months (Fig. 1, hereafter referred to as the migratory peak). We pooled data for *A. statira* and *Aphrissa boisduvalii* Felder because it is difficult to distinguish these species when they are flying freely across the transect lines. Capturing individual butterflies in 7 years between 1994 and 2005, a strong linear

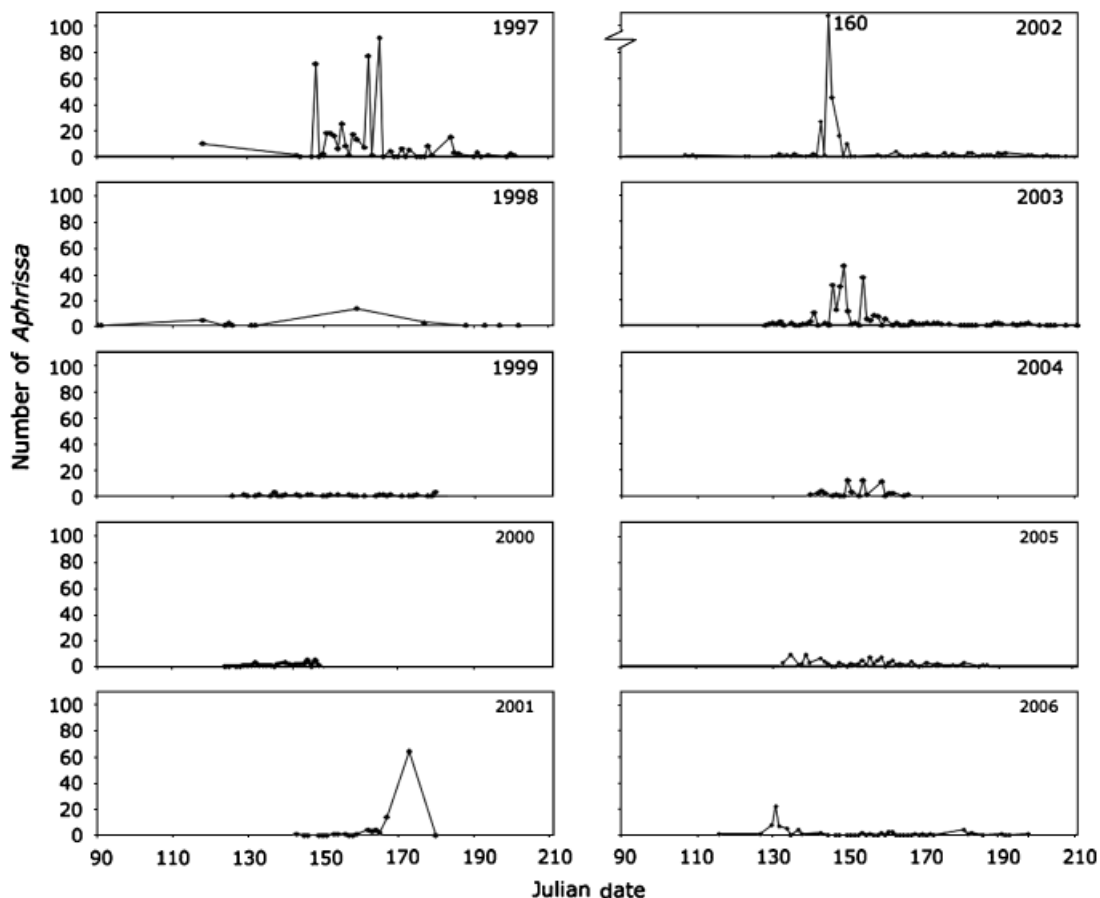


Fig. 1 Observed maximum number per minute of migrating *Aphrissa* butterflies flying south or west across either of two 300 m transects on Lake Gatún, Panama during April–July of 1997–2006. For the migration phenology for 1991–1996, see fig. 1 in Oliveira *et al.* (1998).

relationship between the number of *A. statira* and the total number captured each year ( $R^2 = 0.997$ ,  $P < 0.0001$ ) permits us to reliably estimate that  $89 \pm 2\%$  of the butterflies are *A. statira*. Daily migratory activity patterns generally peak between 10:00 and 12:00 h (see fig. 3 in Oliveira *et al.*, 1998). Because it was not always practical to conduct a census each hour of each day during the migratory season, we sometimes conducted a single census, or more often, two censuses 1 h apart near mid-morning (approximately 10:30–11:30 h) when counts were typically greatest. From the results for a season, we determined the date on which we saw the maximum number of *Aphrissa* butterflies flying across either one of the two transects in the prevailing migratory direction (maximum number of butterflies per minute per 300 m). We call this date the ‘migration peak’ and we call the maximum number of butterflies counted in this peak the ‘maximum migratory rate’. When the maximum migratory rate fell on more than one date, we called the earlier one the migration peak.

#### *Onset of wet season*

We regressed the migration peak on the end of dry season (here referred to as the onset of wet season), a date designated each year by an algorithm created by the Panama Canal Commission and subsequently used by the Meteorological and Hydrological Branch of the Autoridad del Canal de Panama (ACP). The algorithm tracks 11 variables (see [http://striweb.si.edu/esp/physical\\_monitoring/summary\\_seasons.htm](http://striweb.si.edu/esp/physical_monitoring/summary_seasons.htm) for more information). There are no scientific publications justifying its use; however, the need for operators of the Panama Canal to be able to predict over the long term the timing and length of the distinct dry season for a transport system that requires fresh water to operate is obvious. Thus, we assumed that the method employed was a reasonable attempt by those that devised it. Moreover, we benefited from an objective measure of the onset of wet season rather than using our own subjective measurement. The ACP also marks the date that dry season begins each year from which we calculated the length of dry season in days.

#### *Global climate*

As an indicator of ENSO, we used the sea-surface temperature (SST) anomaly from Niño region 3.4 published by the Climate Prediction Center of the National Oceanographic and Atmospheric Administration (<http://www.cpc.noaa.gov/data/indices>). Region 3.4 is located between latitudes  $5^\circ\text{N}$ – $5^\circ\text{S}$  and longitudes  $170^\circ$ – $120^\circ\text{W}$ . The Climate Prediction Center characterizes the SST in this region as critical to characterizing ENSO. The SST anom-

aly is a departure from the adjusted optimum interpolation analysis (measured in  $^\circ\text{C}$ , Reynolds *et al.*, 2002). Information on the base periods used to derive the anomaly may be found on the Climate Prediction Center website (<http://www.cpc.noaa.gov/data/indices/Readme.index.shtml>). We divided the year into four calendar quarters. We used stepwise regression analysis to evaluate relationships between the maximum migratory rate and the mean SST anomalies for calendar quarters 3 and 4 in the year before the migration rate and calendar quarters 1 and 2 in the same year as the migration rate.

#### *Local climate*

As an index of the water available for plant productivity, we used April soil moisture at 30–40 cm depth on BCI. We focused on the month of April because female *Aphrissa* butterflies may be laying eggs on newly flushed leaves. Their offspring will hatch and feed to grow into the migratory generation. Expressed in percent soil wet weight, deep soil moisture was measured by the Terrestrial-Environmental Science Program of the STRI. It is measured gravimetrically from 2.5-cm soil cores collected every 2 weeks at 10 sites in the Lutz watershed. Further details may be found on the STRI website (<http://striweb.si.edu/esp>). We also totaled the rainfall in the BCI laboratory clearing for January through April as a measure of dry season rainfall. These data also came from the Terrestrial-Environmental Science Program of STRI.

As a measure of sunlight available for butterfly thermoregulation and plant productivity, we used total solar radiation measured by a LiCor Pyranometer (LI-COR, Lincoln, NE, USA), and the photosynthetically active radiation (PAR) measured by the Terrestrial-Environmental Science Program above the forest canopy (at the top of Lutz Tower: 42–48 m). We calculated the average daily solar radiation from January through April of each year. January 1991 was excluded because both the pyranometer and the PAR were not functional for the majority of the month, and 1997 lacks PAR values because the data were not recorded for most of February and all of April.

#### *Hostplants*

We monitored new leaf flushing by *C. latifolia* on BCI and along Pipeline Road, approximately 4 km north of Gamboa (for a map of the migratory flyway indicating BCI and Gamboa, see Srygley *et al.*, 1996). Most plants extended up the forest edge to the canopy. With binoculars, we observed 10 branches for each plant and counted the number that were flushing new leaves. *A. statira* butterflies are not active in the forest interior, and so the proportion is a relative assessment of the availability of

new leaves for larval diet. Plants were added or subtracted as they were discovered, died, or lost (on average, 4.6 plants were monitored at any one time). We observed the plants approximately once each month from January 1995 to December 1997 (Fig. 2a). In 2002–2006, we monitored the same plants every 2 weeks concentrating our efforts on the migration period (early April to the end of July, Fig. 2b). We averaged the plants' flushing proportions on each date sampled. We then found the maximum for each year and called that date the peak flushing date and the quantity the peak proportion.

*X. seemannianum* was monitored for flushing of new leaves along Pipeline Road. It too is a canopy liana, and so we observed plants from the road edge. We discovered *A. statira*'s use of *Xylophragma* in November 1994 and we began to monitor these hostplants at that time. Data were collected in the same way as that for *C. latifolia*. On average, 5.6 plants were monitored once each month, year-round from January 1995 to December 1997 (Fig. 2c). In 2002–2006, we monitored five plants every 2 weeks during the migration period (Fig. 2d). Because none of the plants produced new leaves during the migration period in 1996, we did not assign a peak flushing date for *Xylophragma*. For that year, the peak proportion was zero.

## Results

### Global and local climate

Over the past 100 years, the average date that wet season began was May 4. Over the course of this study ( $n = 16$  years), the average onset of wet season was May

10 and ranged between April 24 and June 7. The date that wet season began was significantly related with the migration peak (Fig. 3a,  $F_{1,14} = 5.56$ ,  $y = 27 + 0.5x$ ,  $P = 0.034$ ). The migration peak occurred approximately 4 weeks after the onset of wet season (mean  $SD = 32.2 \pm 12.1$  days). The migration peak was later when dry season was longer ( $F_{1,14} = 5.10$ ,  $P = 0.040$ ) and sunnier (Pyranometer:  $F_{1,14} = 7.05$ ,  $P = 0.0188$ ; PAR:  $F_{1,14} = 12.22$ ,  $P = 0.0039$ ). The migration peaked earlier when deep soil on BCI was more moist in April (Fig. 3b,  $F_{1,14} = 5.43$ ,  $P = 0.035$ ).

The maximum migratory rate of *Aphrissa* butterflies was not significantly autocorrelated from 1 year to the next ( $r = 0.26$ ). However, it tended to be negatively correlated across a 2-year lag (partial correlation =  $-0.50$ ). The median maximum migratory rate was 22 butterflies per minute per 300 m, yet in 3 years, 1992, 1997, and 2002, counts exceeded 90 per minute.

Log-transformed maximum migratory rate of *Aphrissa* was best explained by the ENSO 3.4 SST for the second quarter (Fig. 4,  $F_{1,14} = 8.17$ ,  $P = 0.013$ ). The other quarters were not significant ( $P > 0.91$ ) following selection of the ENSO 3.4 SST for the second quarter. However, the ENSO 3.4 SST anomaly was highly autocorrelated among calendar quarters, although only within half-years across the duration of this study. The partial correlation among contiguous quarters was 0.75 ( $P < 0.0001$ ) and it was  $-0.50$  among half-year lag times ( $P < 0.0001$ ), whereas three- to eight-quarter lags were not significant ( $P > 0.15$  in all cases). Thus El Niño events, which often begin in October and end in the first half of the following year, are independent across years within the duration of this study. However, the

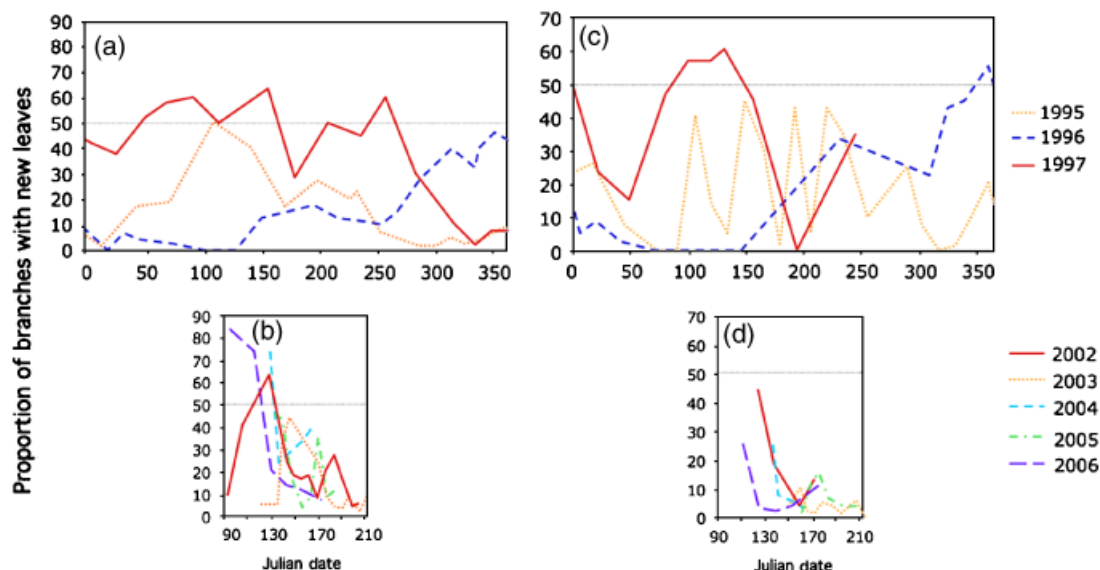
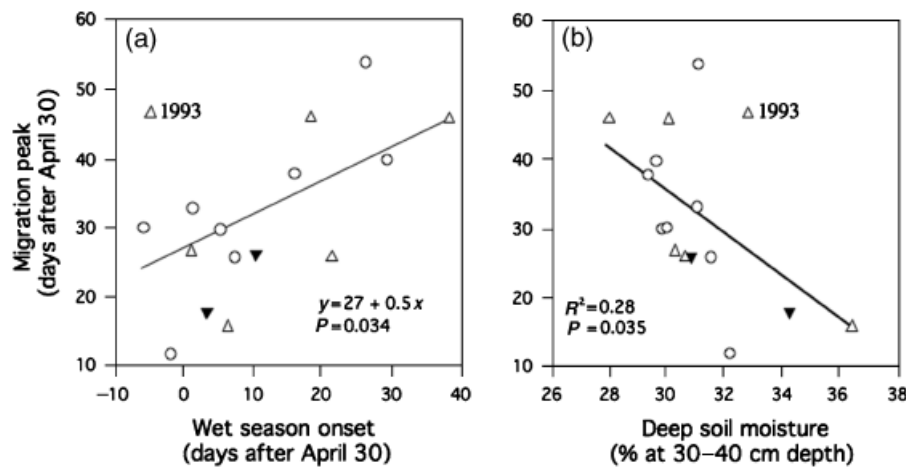


Fig. 2 New leaf-flushing activity for (a, b) *Callichlamys latifolia* and (c, d) *Xylophragma seemannianum* (Bignoniaceae), larval hostplants for *Aphrissa statira*. Hostplants were monitored all year for 3 years (a, c), and then during the migration season (April–July) for 5 years (b, d).



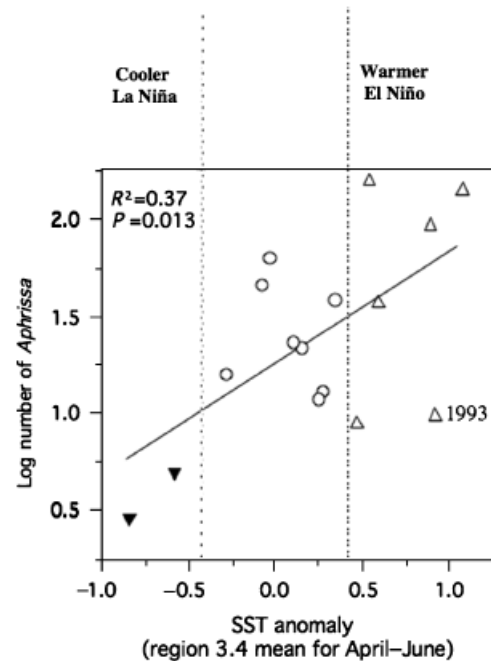
**Fig. 3** The date that the migratory rate of *Aphrissa* butterflies peaked each year was positively associated with (a) the onset of wet season for the same year (data courtesy of the Panama Canal Authority) and negatively associated with (b) deep soil moisture on Barro Colorado Island (BCI) in April. Dates are graphed as days relative to the end of April, which is near to the 100-year average for the onset of wet season (May 4). Open triangles indicate El Niño years; closed triangles, La Niña years; open circles, neither El Niño nor La Niña years.

autocorrelations indicate that associating maximum migratory rate of butterflies with the ENSO 3.4 SST in the second quarter may also indicate a much more general association with the ENSO event that spans from the latter quarter of the previous calendar year to the first or second quarter of the year of interest. Across the course of this study, the mean ENSO 3.4 SST anomaly in the second quarter of the year (April–June) was 0.23. With warm SST anomalies ( $>0.4^{\circ}\text{C}$  above average), the years 1991, 1992, 1993, 1997, and 2002 are classified as El Niño events (1997 was a very strong event). Defining La Niña events as a cold SST anomaly ( $<0.4^{\circ}\text{C}$  below average), the year 1999 was a strong event and 2000 a weak one.

The maximum migratory rate declined exponentially with increased deep soil moisture on BCI in April (Fig. 5a,  $F_{1,14} = 6.95$ ,  $P = 0.020$ ). The maximum migratory rate also declined exponentially with total dry season precipitation (Fig. 5b,  $F_{1,14} = 5.18$ ,  $P = 0.039$ ), which in turn declined significantly with the ENSO 3.4 SST in the second quarter ( $F_{1,14} = 5.43$ ,  $P = 0.035$ ). The ENSO 3.4 SST was not significantly related to solar radiation in the dry season (Pyranometer:  $F_{1,14} = 0.09$ ,  $P = 0.765$ ; PAR:  $F_{1,13} = 0.50$ ,  $P = 0.494$ ). Total solar radiation did not significantly effect the maximum migratory rate (Pyranometer:  $F_{1,14} = 0.58$ ,  $P = 0.459$ ), but PAR did tend to have an effect on the maximum migratory rate ( $F_{1,13} = 4.04$ ,  $P = 0.066$ ).

#### Hostplant new leaf phenology

For *X. seemannianum*, the mean proportion of branches producing new leaves declined significantly with rainfall in the dry season (measured locally in Gamboa, Fig. 6a,  $F_{1,6} = 7.70$ ,  $P = 0.032$ ) and increased signifi-



**Fig. 4** The log-transformed maximum migratory rate for *Aphrissa* butterflies relative to the average sea-surface temperature (SST) anomaly measured in Nino region 3.4 in the second quarter of the year (data courtesy of the National Oceanographic and Atmospheric Administration). Symbols explained in Fig. 3 legend.

cantly with the ENSO index in the second quarter (Fig. 6b,  $F_{1,6} = 9.26$ ,  $P = 0.023$ ). It was not significantly related to total solar radiation or PAR in the dry season or in April ( $P > 0.34$  for all four tests). For *C. latifolia*, the mean proportion of branches producing new leaves tended to decrease with rainfall on BCI (Fig. 6c,

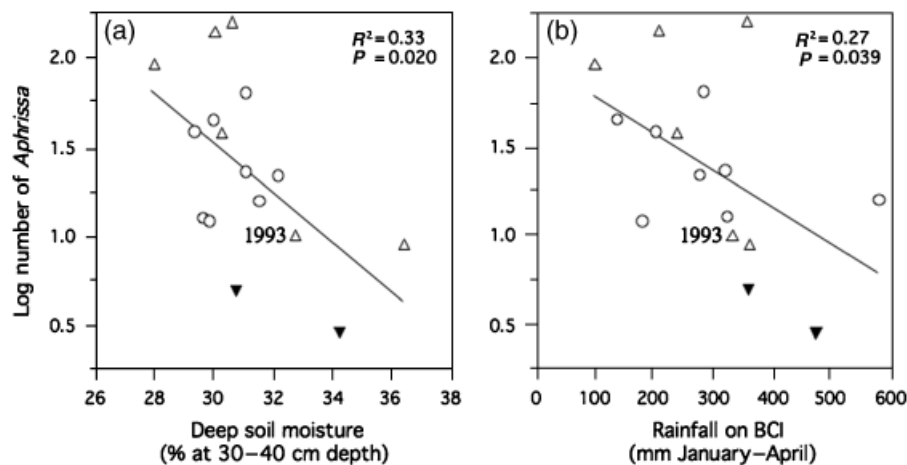


Fig. 5 (a) The maximum migratory rate for *Apherissa* butterflies declined logarithmically with deep soil moisture on Barro Colorado Island (BCI) in April, and (b) the total rainfall during the dry season. Symbols explained in Fig. 3 legend.

$F_{1,6} = 3.77$ ,  $P = 0.100$ ), but it was not significantly associated with the ENSO 3.4 SST (Fig. 6d,  $F_{1,6} = 2.02$ ,  $P = 0.205$ ). It too was not significantly related to solar radiation in the dry season or in April ( $P > 0.34$  for all tests).

The maximum migration rate of *Apherissa* was not related to the peak amount of new leaf production in *Callichlamys* ( $F_{1,6} = 0.31$ ,  $P = 0.60$ ), but it tended to increase with the peak amount of new leaf production in *Xylophragma* ( $F_{1,6} = 3.59$ ,  $P = 0.107$ ). The *Apherissa* migration peaked approximately 22 days after *Callichlamys* peaked flushing ( $F_{1,6} = 6.65$ ,  $y = 22 + 0.37x$ ,  $P = 0.042$ ), whereas it was not related to the peak flushing of *Xylophragma* ( $F_{1,5} = 0.00$ ,  $P = 0.99$ ).

## Discussion

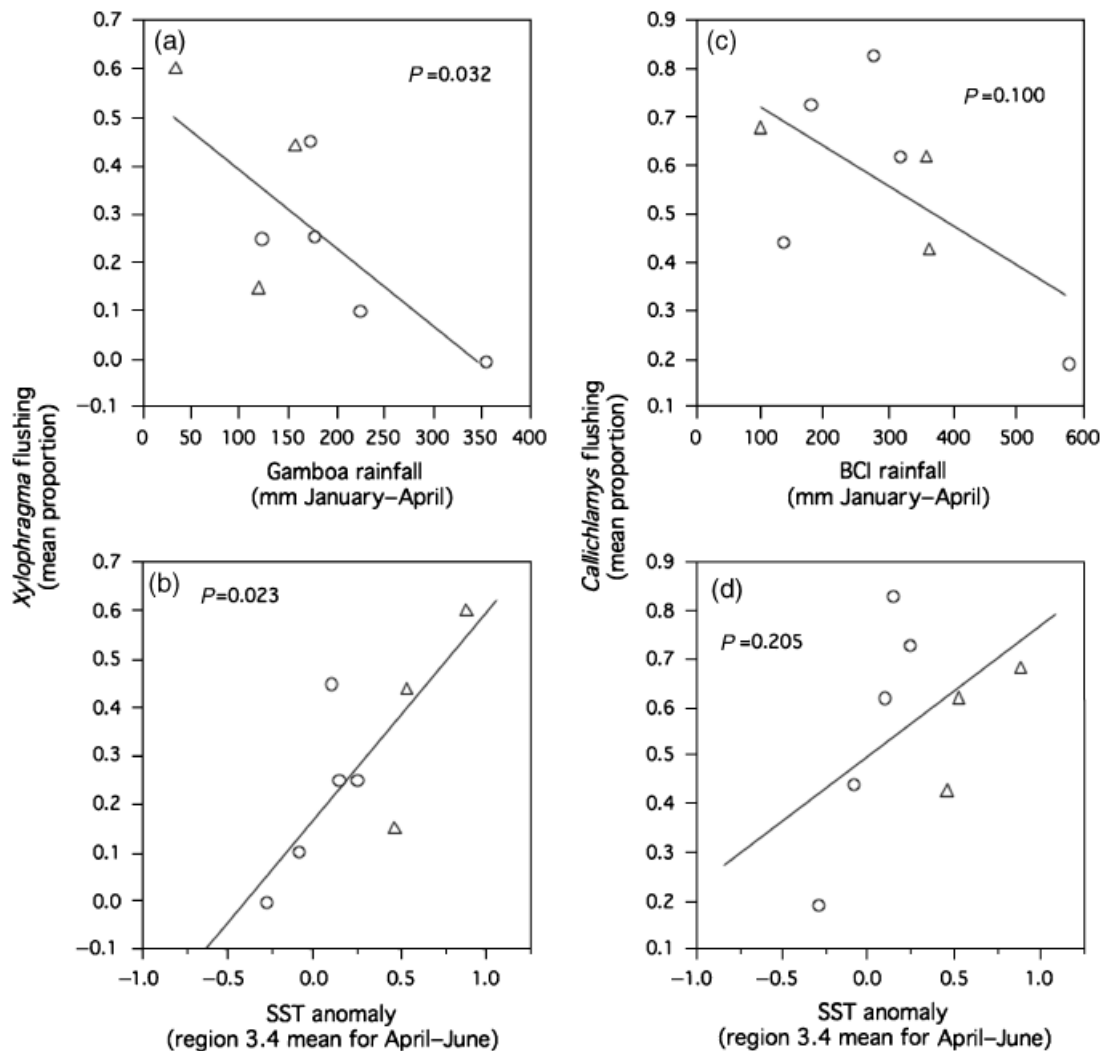
The migration of *Apherissa* butterflies across the Panama Canal peaked approximately 4 weeks after the onset of wet season. *A. statira* grew from egg to adult in approximately 22 days when reared in the laboratory (R. B. Srygley, unpublished data). From these observations, we hypothesize that in the first 4 or 5 days following the initiation of wet season, females lay eggs on newly flushed leaves. These eggs grow into a new generation of adults that migrate from the wetter evergreen Atlantic coastal forests to the drier deciduous forests on the Pacific coast.

The maximum migratory rate was strongly influenced by the ENSO. The maximum migratory rate was greatest during drier El Niño events and least during wetter La Niña events. The ENSO climate is known to affect herbivore populations in subtropical desert and seasonally dry grasslands and scrub forests. Some of the best documented are the increases in rodent populations as a result of increased rainfall during El

Niño years causing a pulse of plant productivity in scrub and desert communities of western South America (Meserve *et al.*, 2003) and western North America (Polis *et al.*, 1997; Holmgren *et al.*, 2006). Painted-lady butterflies *Vanessa cardui* also migrate in greater numbers following rainy El Niño events in the western United States (Vandenbosch, 2003). Thus the typical scenario in these dry regions is a pulse in plant productivity positively affecting herbivore populations. However in the case of the rodents, Meserve *et al.* (2003) conclude that control shifts from bottom-up in dry years when plant resources are limited to top-down in wetter years marked by greater primary productivity. Similarly, breeding success of rufous-crowned sparrows in California scrub habitat was also subject to control shifting from bottom-up during dry, resource-limited La Niña to top-down during wet El Niño (Morrison & Bolger, 2002). In the Mediterranean climate of California, increased rainfall suppresses herbivory by the ghost moth *Hepialis californicus* because wet soils favor the nematodes that regulate the moths (Preisser & Strong, 2004). A variety of ecological effects may thus derive from systematic changes in rainfall.

In addition to influencing the maximum migratory rate, we assume that ENSO affects the population sizes of migratory butterflies at the Atlantic coastal source and the Pacific destination of this migration. Populations of other lepidopteran species in Panama erupted during the strong El Niño event of 1997–1998 (e.g., in the Pacific coastal dry forest, Van Bael *et al.*, 2004; and the Atlantic coastal wet forest, J. Wright, unpublished data).

There are a number of mechanisms that could lead to an outbreak in the *Apherissa* populations in El Niño years and a decline in La Niña years. El Niño years are associated with increased temperatures, increased solar



**Fig. 6** The maximum proportion of *Xylophragma* branches flushing new leaves (a) declined with total local rainfall during the dry season and (b) increased with the sea-surface temperature (SST) anomaly for region 3.4 in the second quarter. The maximum proportion of *Callichlamys* branches flushing new leaves tended to have the same relationships as *Xylophragma* with (c) dry season rainfall and (d) the SST anomaly. Symbols explained in Fig. 3 legend.

radiation, and decreased rainfall on BCI (Wright & Calderón, 2006). *X. seemannianum*, the bignoniaceous liana that is a host for *A. statira* responded to the decreased rainfall during the dry season and dry April soils associated with El Niño with an increase in leaf flushing. *C. latifolia*, the other known host for *A. statira*, had its greatest leaf production during intermediate years of moderate dry season rainfall. Measuring seed production, Wright & Calderón (2006) found that *Callichlamys* and other lianas responded favorably to El Niño years as long as they did not result in extreme droughts. Given the general effect of water stress on plant productivity in tropical wet forest (e.g., Engelbrecht & Kursar, 2003), it is surprising that the lianas respond so favorably to dry soils.

We propose two hypotheses to explain the increase in plant productivity with El Niño years in this tropical wet forest. First, the host lianas may produce new leaves more synchronously at the onset of wet seasons that end droughts associated with El Niño years. Our observations do not support this hypothesis. In 3 out of 7 years, *Xylophragma* peaked before the wet season began. Factors timing leaf production in these host lianas are not known, and threshold levels of drought can synchronize flowering and enhance seed set in some tropical forest plants (Alvim, 1960).

Second, greater availability of light for photosynthesis during El Niño relative to La Niña years may promote the production of new leaves. This hypothesis is supported by observations that solar radiation limits



photosynthetic activity in Neotropical wet forest (reviewed in Van Schaik *et al.*, 1993), and experimental addition of radiation to a Pacific coastal forest during the wet season resulted in increased tree growth and reproduction (Graham *et al.*, 2003). Moreover, Amazonian rainforests produce and drop leaves in anticipation of seasonal changes in solar radiation (Myneni *et al.*, 2007). Although dry season sunlight measured above the canopy on BCI during the period of our study was unaffected by El Niño (but see Wright & Calderón, 2006), drought may cause big trees to lose leaves and the thinned canopy may allow more sunlight onto the host lianas. On BCI, understory *Connarus turczaninowii* lianas also responded positively to the duration of the dry season (Aide & Zimmerman, 1990), which the authors postulate is due to greater canopy tree leaf loss during El Niño years reducing competition for water and light in the understory.

For this study, we did not measure hostplant quality or predation pressure, both of which may contribute to population outbreaks. As a result of poor defense in drought years, hostplants might also suffer greater herbivore pressure and the insects might survive better during development. Because of increased solar radiation, El Niño years might be favorable for herbivore development, or adults might be more active to find food plants or oviposit on larval resources. El Niño might also result in a decrease in the natural enemies of herbivores, resulting in an ecological release of the lepidopteran populations (e.g., Preisser & Strong, 2004). Thus our demonstration that outbreaks in migratory populations of *Aphrissa* butterflies is associated with increased plant productivity in Panama does not preclude potential roles of plant defenses and top-down pressure from parasitoids and predators in regulating migratory populations (Stireman *et al.*, 2005).

In Panama, an El Niño year is typically characterized by drier than normal conditions, and the *Aphrissa* butterflies respond with an outbreak in the migratory population. The El Niño year of 1993 was a notable exception. The rate of butterflies migrating was much lower than predicted by its ENSO index (Fig. 4). However, in Panama the dry season of 1993 was unusually wet for an El Niño year. When deep soil moisture in April is the predictor, the maximum migratory rate for 1993 falls in line (Fig. 5a). Thus, both global and local environmental factors influenced the number of migrants traversing the Panama Canal.

In the Meteorological Research Institute model to predict climate change, ENSO becomes more extreme in its peaks with an overall warming of the mean SST; however, this is not true for the Geophysical Fluid Dynamical Laboratory model (Yeh & Kirtman, 2007). Thus, extreme El Niño and La Niña years may become

more frequent. Other tropical rainforest Lepidoptera appear to have a similar response to rainfall as the *Aphrissa* butterflies in Panama (e.g., Van Bael *et al.*, 2004; Kunte, 2005). If this phenomenon extends beyond Lepidoptera, then insect outbreaks during El Niño and population crashes during La Niña may become more frequent. Over the past century, the numbers of Lepidoptera migrating to Britain were associated with higher temperatures in the migratory route in phase with the North Atlantic Oscillation (Sparks *et al.*, 2005). Similarly, a long-term increase in the number of migrants may be linked to global warming (Sparks *et al.*, 2007).

The El Niño migration syndrome may apply to desert, savannah, and tropical wet forest (e.g., Vandenbosch, 2003), but the mechanisms may differ. In El Niño years, rainfall in deserts and savannah tends to increase, while it declines in tropical wet forests (see fig. 1 in Holmgren *et al.*, 2006). However in all three ecotypes, hostplants respond by producing more leaves, enhancing migratory butterfly populations.

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