El Niño, Host Plant Growth, and Migratory Butterfly Abundance in a Changing Climate

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ABSTRACT

In the wet forests of Panama, El Niño typically brings a more prolonged and severe dry season. Interestingly, many trees and lianas that comprise the wet forests increase their productivity as a response to El Niño. Here, we quantify the abundance of migrating *Marpesia chiron* butterflies over 17 yr and the production of new leaves of their hostplants over 9 yr to test the generality of the El Niño migration syndrome, *i.e.*, whether increased abundance of migrating insects and productivity of their food plants are associated with El Niño and La Niña events. We find that the quantity of *M. chiron* migrating across the Panama Canal was directly proportional to the sea surface temperature (SST) anomaly of the Pacific Ocean, which characterizes El Niño and La Niña events. We also find that production of new leaves by its larval host trees, namely *Brosimum alicastrum*, *Artocarpus altilis*, and *Ficus citrifolia*, was directly proportional to the SST anomaly, with greater leaf flushing occurring during the period of the annual butterfly migration that followed an El Niño event. Combining these and our previously published results for the migratory butterfly *Aphrissa statira* and its host lianas, we conclude that dry season rainfall and photosynthetically active radiation can serve as primary drivers of larval food production and insect population outbreaks in Neotropical wet forests, with drier years resulting in enhanced plant productivity and herbivore abundance. Insect populations should closely track changes in both frequency and amplitude of the El Niño Southern Oscillation with climate change.

Abstract in Spanish is available in the online version of this article.

Key words: climate change; drought; ENSO; phenology; plant–insect interaction; tropical rain forest.

RANGE AND PHENOLOGICAL SHIFTS OF BUTTERFLIES HAVE BEEN MODELS FOR THE EFFECTS of environmental change on other insect species (Parmesan 2006). However, the effects of climate change on insect range and phenology have been researched primarily in temperate zones of the northern hemisphere (Parmesan 2007), where monitoring of populations has occurred over longer periods and broader geographic areas. Tropical habitats harbor far greater insect diversity than temperate ones (Novotny *et al.* 2006), and a major gap in our knowledge is how climatic effects influence these tropical insect populations (*e.g.*, Stireman *et al.* 2005).

Tropical forests worldwide are experiencing an increase in ambient temperature, and in many regions the severity and duration of seasonal drought have also increased (Malhi & Wright 2004). In the Neotropics, the El Niño Southern Oscillation (ENSO) is a primary driver of temperature and rainfall (Foley *et al.* 2002), with El Niño events typically associated with more extended and severe droughts (Lyon 2004). El Niño events almost always span two calendar years, beginning in March to September of the first year, becoming most severe in November to January, and extending to February or March of the second

year (Trenberth 1997). If, on average, the severity and duration of seasonal drought continue to increase in the future, then current El Niño events may provide a useful contemporary snapshot into the response of tropical forest communities to climate change (Coley 1998).

In the wet forest of Barro Colorado Island (BCI) in central Panama, El Niño events typically bring an increase in solar radiation and ambient temperature and a reduction in precipitation (Leigh 1999). Annual tree ring data from central Panama suggest that El Niño events may enhance tree growth, flowering, and seed production, although extreme El Niño events may be detrimental to reproduction (Condit *et al.* 2004, Wright & Calderón 2006). Lianas also grow more in central Panama during drier El Niño years (Srygley *et al.* 2010, Schnitzer & Bongers 2011). The influence of the ENSO on primary productivity (Behrenfeld *et al.* 2001, Stenseth *et al.* 2002, McPhaden *et al.* 2006) careens upward into higher trophic levels, resulting in periodic outbreaks of herbivorous species (Vandenbosch 2003, Holmgren *et al.* 2006). For example, greater leaf productivity by larval host lianas during El Niño in Panama is associated with greater abundance of migrating adult *Aphrissa statira* butterflies, with the greatest larval damage to the hostplants occurring during the first 4 wk of the wet season (Srygley *et al.* 2010).

This pattern of increased primary productivity resulting in insect outbreaks and migration during El Niño years – which is common to many deserts, savannas, and tropical wet forests – is called the El Niño Migration Syndrome (Srygley *et al.* 2010). For deserts and savannas, rainfall tends to increase during El Niño events and leads to a pulse in plant productivity (Polis *et al.* 1997, Meserve *et al.* 2003, Holmgren *et al.* 2006), whereas in tropical wet forests, rainfall tends to decrease during El Niño events. More resistant to drought than many evergreen trees (Schnitzer & Bongers 2011), lianas respond by producing more leaves, and the butterflies that feed on them increase in abundance (Srygley *et al.* 2010).

Here, we determine if the El Niño Migration Syndrome in tropical wet forests applies only to *A. statira* and its host lianas, or if it can be more generally applied to other herbivorous species. We investigate the many-banded daggerwing, *Marpesia chiron*, a sympatric butterfly species distantly related to *A. statira*, and with very different larval hostplants. We relate 17 yr of migratory abundance data and 9 yr of hostplant phenology data from Neotropical wet forests to the ENSO, and also investigate temporal variation in hostplant productivity across a rainfall gradient as a potential driver of the migration. Finally, we briefly review the behavior of ENSO in the past and its future forecasting to predict how these Neotropical wet forest plants and insects might respond to climate change.

METHODS

STUDY ORGANISMS.—Annually in May to August, *Marpesia chiron* Fabricius (Nymphalidae) butterflies migrate directionally across Lake Gatún near BCI (9°10′N, 79°51′W), the site of a biological field station in the Barro Colorado Nature Monument administered by the Smithsonian Tropical Research Institute (STRI). By maintaining their track when blown off course by the wind, *M. chiron* shows goal-oriented behavior (Srygley & Dudley 2008), with the predominant migratory direction at this time of year being south by southwest (Fig. S1). Thus, the direction and timing of the migration are similar to that for *A. statira* (Pieridae), with the migratory flyway of both taxa extending across the isthmus of Panama in the region of the Panama Canal. This region is characterized by a rainfall gradient from the Atlantic coastal wet forest to the Pacific coastal dry forest. Across the isthmus, a distinct dry season occurs from around mid-December to end-April, during which only one-tenth of the annual rain falls (dry season average: 300 mm on the Atlantic coast, and 140 mm on the Pacific coast in Panama City).

As is the case for many tropical insects, the larval foodplants for *M. chiron* are still being discovered. DeVries (1987) notes four genera in the mulberry family (Moraceae) as hostplants: *Brosimum*, *Ficus*, *Artocarpus*, and *Chlorophora* (*Maclura*). Beccaloni *et al.* (2008) compiled hostplant records for *M. chiron*, listing when determinations were made to species: *Artocarpus heterophyllus*, *A. integrifolia*, *Brosimum alicastrum*, *B. lactescens*, *Ficus benjamina*, *F. carica*, *F. pumila*, *Maclura pomifera*, *M. tinctoria*, *Morus alba*, *Mo. nigra*, all of which are in the Moraceae. *Zanthoxylum rhoifolium* (Rutaceae) and an uniden-

tified Urticaceae are listed as erroneous records (Beccaloni *et al.* 2008). Use by *M. chiron* of different hostplant genera, including a non-native to the Neotropics, suggests that the butterfly is a generalist feeder on Moraceae. This range of diet, however, may also reflect differences in hostplants among butterfly populations. For 3 yr, we surveyed new leaf growth of breadfruit *Artocarpus altilis* and *Brosimum alicastrum* for *M. chiron* eggs and larvae, and we surveyed new leaves of *F. citrifolia*, *F. colibraina*, *F. obtusifolia*, *F. pertusa*, *F. perforate*, and *F. trigonata* for 8 yr. The only trees on which *M. chiron* eggs or larvae were ever observed on our study sites were *F. citrifolia* and *F. obtusifolia*, and for the restricted period of May–June 2002. The single egg found on *F. obtusifolia* was not reared and those on *F. citrifolia* disappeared (probably predated by ants) except for one, which was collected and reared in the laboratory. Thus, *F. citrifolia* is the only confirmed hostplant for *M. chiron* in Panama, but note that the chance of encounter is low (*e.g.*, the rapid disappearance of eggs from *F. citrifolia* patrolled by ants). Reports of *M. chiron* on *B. alicastrum* in neighboring Costa Rica (DeVries 1986, http://Janzen.sas.upenn.edu) suggest that this tree may also be a larval foodplant in Panama. *Marpesia chiron* adults nectar at diverse flowers, and are also attracted to rotting fruits.

MIGRATORY DIRECTIONS.—From 0943 h to 1030 h on 29 May 2002, we collected vanishing bearings of butterflies that flew by an observer standing on a bridge over the Guanché River on the Atlantic coast. The observer would run to intercept a butterfly's track, and from that point, use a Sigma sighting compass to take the bearing of the point where the butterfly vanished from sight. Between 28 May–6 June 2003, we used standard methods to measure butterfly tracks across Lake Gatún (Srygley *et al.* 1996). A pilot in a small boat matched the speed and direction of a selected butterfly flying across the lake. Then from the boat, a second person measured the butterfly's direction with a sighting compass. At least twenty bearings were collected at each location. We calculated the mean orientation (μ) and used Rayleigh's test to compare the data at a location with the null hypothesis of a uniform distribution. Mean orientations on the Atlantic coast and the center of the isthmus were compared with Watson–William's *F*-test.

CENSUSING MIGRATORY BUTTERFLIES.—During each migratory season, we counted the number of butterflies flying across two 300 m transects over Lake Gatún, an artificial lake that forms a large section of the Panama Canal. We observed butterflies from a boat tied to a stump at the southwest apex of the two transects (9°10′622″N, 79°49′873″W; for methodology details, see Srygley *et al.* 2010). Here, we focus on the maximum migratory activity of *M. chiron* over the course of the migratory months (Fig. S2). From censuses for each season, we determined the date we saw the maximum number of *M. chiron* flying across one of the two transects (maximum number of butterflies per minute per 300 m). This date is termed the migration peak, and the maximum number is termed the maximum migratory rate. If the same maximum rate fell on more than one date, we called the earlier one the migration peak.

GLOBAL AND LOCAL CLIMATE.—For comparison with results for *A. statira* and its hostplants, we use the same indicator of ENSO, measures of local climate, and the onset of the wet season (for details, see Srygley *et al.* 2010). As an indicator of ENSO, we used the sea surface temperature (SST) anomaly (measured in °C, Reynolds *et al.* 2002) from Niño region 3.4, located between latitudes 5°N and 5°S and longitudes 120–170°W. The Climate Prediction Center (http://www.cpc.ncep.noaa.gov/data/indices) characterizes the SST in this region as critical to characterizing warm (> +0.5°C) El Niño and cold (< −0.5°C) La Niña episodes. We use stepwise regression analysis (alpha = 0.10 to enter, Kleinbaum *et al.* 1988) to evaluate relationships between the maximum migratory rate and the mean SST anomalies for calendar quarters 3 and 4 in the year prior to the migration rate, and for calendar quarters 1 and 2 of the same year.

We used April soil moisture at 30–40 cm depth on BCI as an index of water availability to plants. We also totaled rainfall for January to April as a measure of dry season rainfall, and we calculated the average daily solar radiation from January to April of each year using both pyranometer and photosynthetically active radiation (PAR) values. The Terrestrial Environmental Science Program of STRI collected the environmental data. Wet season onset is based on an algorithm created by the Panama Canal Commission (see Srygley *et al.* 2010 for justification).

HOSTPLANT PHENOLOGY.—From January 1995 to December 1997, we measured new leaf flushing by *B. alicastrum* (mean $N = 3$, range 2–5) and by *A. altilis* on Gigante Peninsula in the Barro Colorado Nature Monument and in Gamboa (mean $N = 2.3$, range 2–3). Using binoculars when required, we scanned 10 branches of each tree to count the proportion of branches that were flushing new leaves. For one small individual of *A. altilis*, we were limited to the proportion of three branches. We scanned branches exposed to sunlight because *M. chiron* rarely fly into the forest understory (Srygley & Chai 1990). So, the mean proportion is a relative assessment of the availability of new leaves for oviposition and larval feeding. Trees were added or subtracted as they were discovered, died, or lost. We scanned trees approximately once a month. From 2002 to 2006, we focused on *F. citrifolia* because it was the only species on which we found *M. chiron* feeding. We observed trees (mean $N = 4.8$, range 2–6) every 2 wk during the migration period (generally April–July). We did not monitor *B. alicastrum* and *A. altilis* in the latter 5 yr when focusing on *F. citrifolia*.

Because the direction and timing of the migration are similar to that of *A. statira*, we use the same working hypothesis for *M. chiron* that the south by southwesterly migration results from limited hostplant leaf production during the wet season in the evergreen Atlantic coastal forest due to overcast skies (*i.e.*, light limitation hypothesis, Van Schaik *et al.* 1993, Graham *et al.* 2003). As a result of the sudden reduction in new growth upon which the larvae can feed, we hypothesize that adult females find fewer suitable oviposition sites and eggs and larvae become more crowded on the remaining new growth. In response, newly enclosed butterflies migrate toward the deciduous forest of the Pacific coast, where the greater availability of sunlight permits

trees to continue to flush new leaves (Srygley & Oliveira 2001). To test this hypothesis, we compared new leaf flushing for breadfruit (*A. altilis*) on the Atlantic coast near Colon and Portobelo with new leaf flushing in the center of the isthmus (Gigante Peninsula and Gamboa). The same methods were used to census both sets of trees from January 1995 to December 1997, but we did not compare the Atlantic and central locations in 1996 due to temporal gaps in observations of trees on the Atlantic coast during the migration period.

RESULTS

The mean orientation of *M. chiron* butterflies at Guanché River on the Atlantic coast ($N = 25$, $\mu = 206°$, $r = 0.92$, $P < 0.0001$) did not differ significantly from that on Lake Gatún, located in the center of the isthmus ($N = 21$, $\mu = 212°$, $r = 0.89$, $P < 0.0001$; Watson–Williams $F = 0.62$, df = 1,44, $P = 0.44$, Fig. S1).

Over 17 yr (1991–2007), the log-transformed maximum migratory rate of *M. chiron* censused each year was proportional to that for *A. statira* ($r = 0.673$, $P = 0.0028$, Fig. 1A). However, at peak abundance each year, the number of *M. chiron* was, on average, only one-tenth that of migrating *A. statira*. Log-transformed maximum migratory rate of *M. chiron* was best explained by the ENSO 3.4 SST for the first quarter ($F_{1,15} = 4.10$, $P = 0.061$, Fig. 1B). The maximum migratory rate declined with increasing April deep soil moisture measured on BCI ($N = 17$, $F_{1,15} = 6.36$, $P = 0.024$, Fig. 2A), but not with total rainfall on BCI during the dry season (January to April: $F_{1,15} = 2.14$, $P = 0.16$). Total solar radiation did not have a significant effect on maximum migratory rate ($F_{1,15} = 0.94$, $P = 0.35$), but the maximum migratory rate tended to increase with mean daily dry season PAR (January–April: $F_{1,14} = 4.56$, $P = 0.051$, Fig. 2B). Longer dry seasons were associated with greater maximum migratory rates ($F_{1,15} = 5.31$, $P = 0.036$, Fig. 2C), and the length of the dry season was directly proportional to the ENSO 3.4 SST for the first quarter ($F_{1,15} = 35.79$, $P < 0.0001$, Fig. 3) adding 17 d to the average of 130 d for each degree increase in the SST.

The mean timing of the migration peak was 4 June (range: 10 May–24 June). The date that the migration peaked was not significantly related to the onset of wet season for that year ($F_{1, 15} = 2.27$, $P = 0.153$).

HOSTPLANT LEAF FLUSHING PHENOLOGY.—Leaf flushing by the non-native breadfruit tree *Artocarpus altilis* peaked several times each year and generally peaked twice during the migration season (Fig. S3A). During the migration season, leaf flushing during the La Niña year of 1996 peaked at around half the proportion of branches as during 1995 and 1997. Leaf flushing by the canopy tree *Brosimum alicastrum* also peaked several times each year, but only once during the migration season (Fig. S3B). On average, no more than 10 percent of each tree was producing new leaves during the migration season of 1996, whereas 40–60 percent of the branches were flushing during 1995 and 1997. The strangler fig *F. citrifolia* (Fig. S3C) flushed once during the annual migration
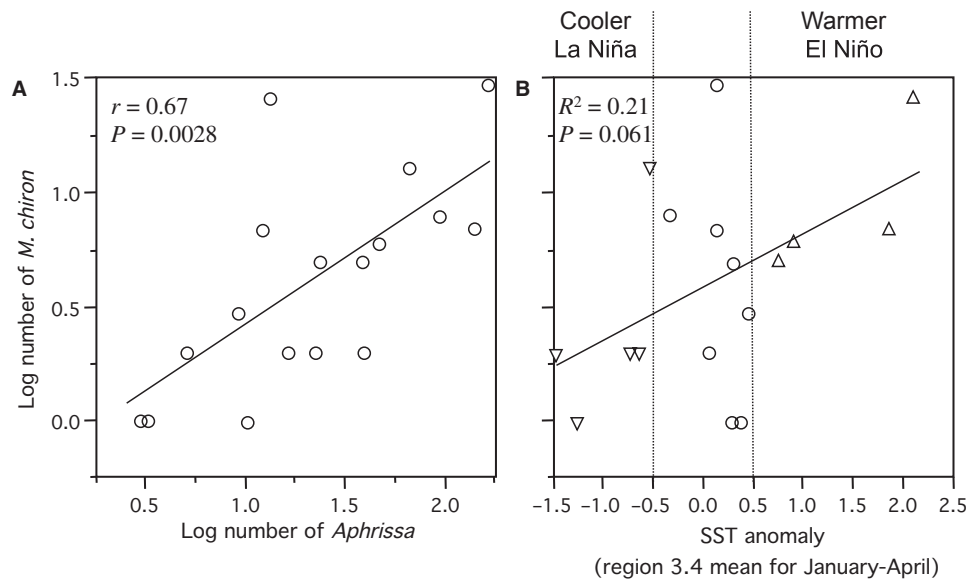
FIGURE 1. Log maximum migratory rate (frequency/minute/300 m) of *Marpesia chiron* crossing the transect over the Panama Canal each year relative to A) the log maximum migratory rate of *A. statira*, and B) the sea surface temperature (SST) anomaly for the first quarter of the same year. SST values > 0.5 correspond with El Niño years (upward pointing triangles), and values < −0.5 correspond with La Niña years (downward pointing triangles). Circles are neither El Niño nor La Niña years.
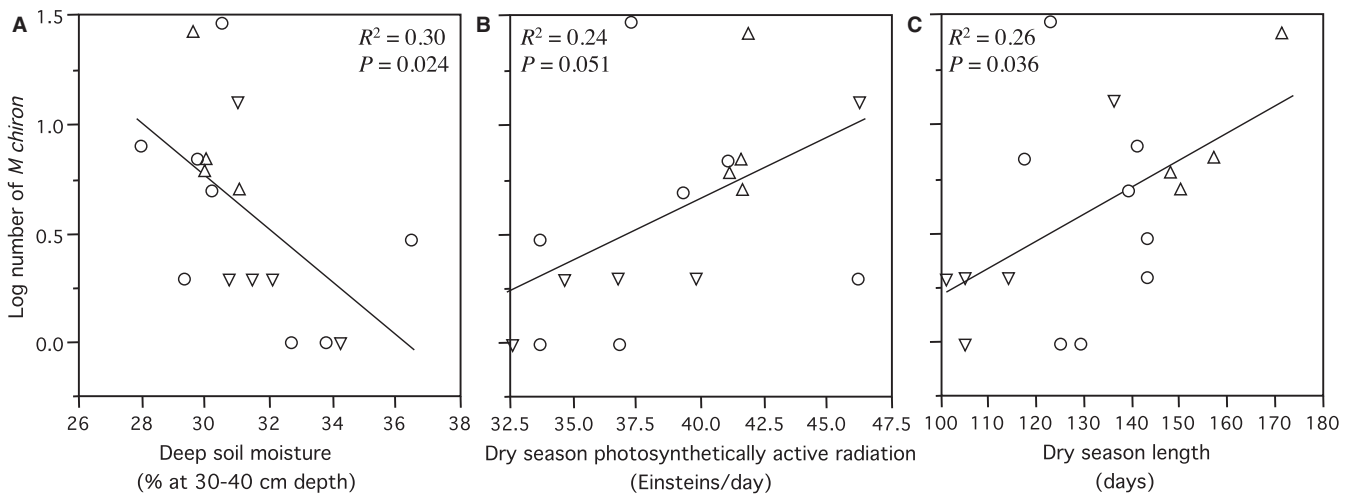

FIGURE 2. Log maximum migratory rate (frequency/minute/300 m) of *Marpesia chiron* relative to (A) mean deep soil moisture on Barro Colorado Island (BCI) in April; (B) mean daily photosynthetically active radiation on BCI during the dry season (January to April); and (C) the length of the dry season for each year.

season. Maximum new leaf production during 2005 averaged 13 percent of all branches (the year that dry season PAR was the least and April soil moisture was the greatest in our sample), well below maxima of 62 percent or more branches for the other 4 yr.

Hostplants did not significantly differ in the maximum percent of branches flushing new leaves during the migration season following adjustment for the ENSO index in the last quarter of the preceding year (ANCOVA: $P = 0.056$ for SST as covariate and $P = 0.264$ for hostplant). Leaf flushing was best explained by the ENSO 3.4 SST for the last quarter of the preceding year ($F_{1,10} = 4.20$, $P = 0.071$, Fig. 4A), but the regression model was only slightly better than selection of the SST in the first quarter of the same year ($F_{1,10} = 4.11$, $P = 0.073$). Hostplant leaf flushing increased significantly with mean daily dry season PAR ($F_{1,7} = 23.13$, $P = 0.0019$, Fig. 4B), but not with total solar radiation ($F_{1,9} = 2.31$, $P = 0.163$). Leaf flushing tended to decline with increasing rainfall during the dry season ($F_{1,9} = 4.66$,
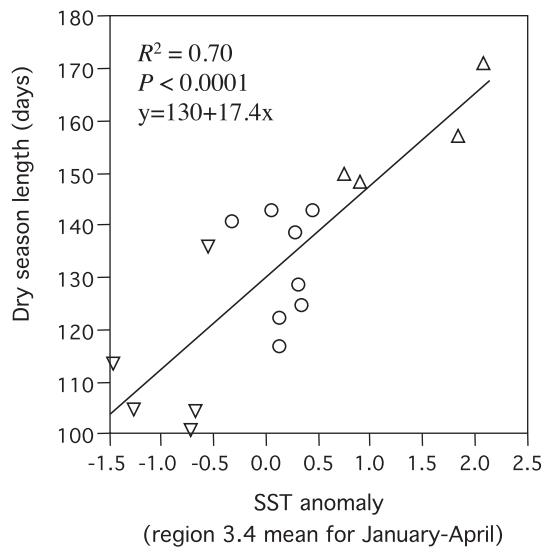
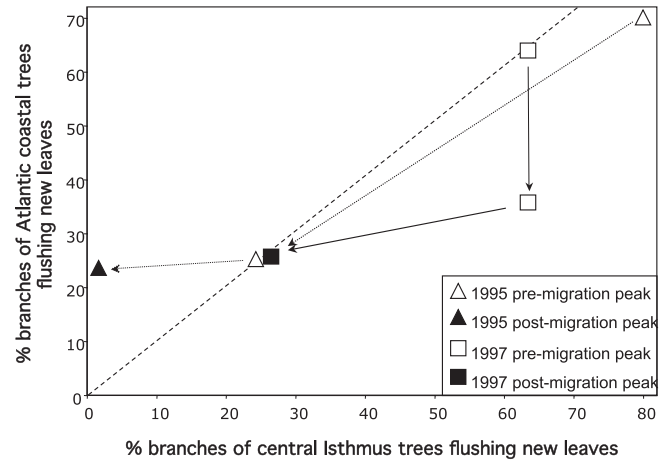FIGURE 3. The increase in dry season length with the SST anomaly for the first quarter of the same year.

FIGURE 5. Phenological overlap of *Artocarpus altilis* on the Atlantic coast and the center of the Isthmus of Panama. The dashed line is drawn where the production of new leaves by trees in the two regions was equal. Points to the left of the line indicate greater production on the Atlantic coast, and points to the right indicate greater production in the center of the isthmus. Arrows are drawn between successive samplings that occur just prior to and after the migration of *M. chiron* peaked in 1995 and 1997 (Julian day 165 and 166, respectively).

$P = 0.059$), and decreased marginally with increasing deep soil moisture in April ($F_{1,9} = 3.76$, $P = 0.084$).

In general, breadfruit trees on the Atlantic coast (Fig. S4) produced more new leaves during the migration period (April–July) than trees in the center of the isthmus. In mid-May, 1995, leaf flushing in the center of the isthmus was slightly greater than on the Atlantic coast (80% relative to 70% of branches, on average), but productivity in the two sites equalized at 25 percent by the end of May (Fig. 5). Following the migration peak of *M. chiron*, the Atlantic coast was producing more leaves due to a decline of leaf production in the center of the isthmus by the latter half of June (23% relative to 2%). In mid-May 1997, leaf flushing on the Atlantic coast and the center of the isthmus were equally high (64%), but by the first week of June, leaf flushing on the Atlantic coast had declined to 36 percent while that in the

center of the isthmus remained high (64%). The migration peaked on 15 June 1997. By the end of July, leaf flushing declined to 26–27 percent in both locations.

DISCUSSION

The maximum migratory rate of *Marpesia chiron* migrating across the isthmus of Panama was influenced by the ENSO. This pattern echoes the effect of the El Niño global climate cycle on the migration of *Aphrissa statira* in Panama (Srygley *et al.* 2010). For both species, the maximum migratory rate was greater during drier El Niño years and least during wetter La Niña years.
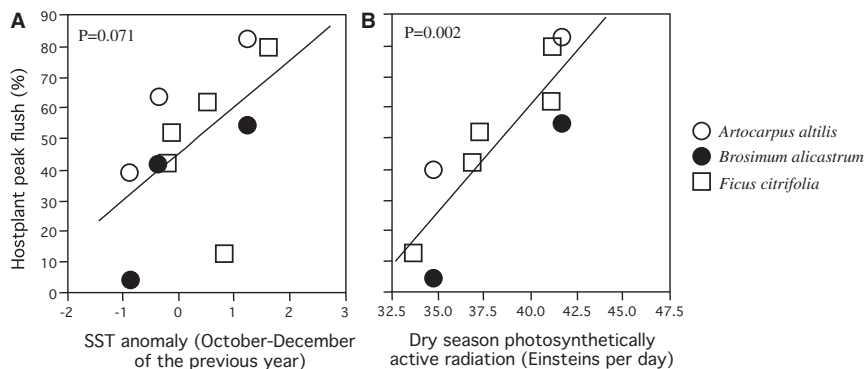

FIGURE 4. The mean proportion of branches flushing new leaves for three hostplants of *Marpesia chiron* combined relative to (A) the sea surface temperature (SST) anomaly for the last quarter of the preceding year; and (B) the mean daily photosynthetically active radiation during the dry season (January–April). *Brosimum alicastrum* and *A. altilis* were measured during 1995–1997, whereas *F. citrifolia* was measured during 2002–2006.

Because the first or second quarters of the current year were best associated with the maximum migratory rates of the butterflies in the same calendar year, we refer to that year as the El Niño or La Niña year although the anomalous events typically begin in the preceding year. These two species are from different butterfly families and as larvae feed on distantly related hostplants: *A. statira* feeds on new leaves of lianas in the Bignoniaceae, and *M. chiron* feeds on new leaves of trees in the Moraceae. With accordingly different lifestyles, these larvae develop into adults that migrate in the same general direction during the same few months of the year. Our results generalize the influences of the ENSO-driven environment on population outbreaks and the physiological and behavioral changes associated with migration.

The maximum migration rate of *A. statira* was strongly associated with the SST anomaly of the second quarter of the year with 37 percent of the variance explained, whereas that of *M. chiron* was associated with the SST anomaly of the first quarter with only 21 percent of the variance explained. Like *A. statira*, the maximum migration rate of *M. chiron* in 1993 was suppressed below that predicted by the ENSO index. Local environmental factors had a greater effect than global climate in the number of *A. statira* migrants traversing the isthmus of Panama (Srygley *et al.* 2010). The dry season of that year was unusually wet, and the abundances of migratory butterflies were much lower than predicted by the ENSO index. One hypothesis consistent with our observations of larval hostplants is that the unusually wet dry season resulted in fewer new leaves upon which the larvae feed relative to a more typical El Niño event. In addition, flowers and fruits upon which the adult butterflies feed were extraordinarily low in 1993 (Wright *et al.* 1999). Moreover, with fewer fruits to ingest, birds and mammals may have eaten more larval and adult butterflies. Also like *A. statira*, the greatest abundance of *M. chiron* counted was in 2002. The count for *M. chiron* was well above that modeled with the first quarter ENSO index (Fig. 2B) when SST was normal, whereas the count for *A. statira* was consistent with the index in the second quarter because the Pacific Ocean had warmed by then to lead into the El Niño event of 2002–2003. The two species differ in that the migratory peak for *A. statira* occurred approximately 4 wk following the onset of wet season, whereas that for *M. chiron* was independent of the beginning of the rains.

The host trees for *M. chiron* responded favorably to drier El Niño events. They flushed more new leaves at their peak between the months of April and July in response to reduced rainfall during the dry season and drier soils in April. Thus, they have similar responses to drought as do the lianas *Callichamys latifolia* and *Xylophragma seemanii* upon which *A. statira* feed (Srygley *et al.* 2010). It appears sea surface temperatures in the Pacific affect these trees and lianas in Panamanian wet forests similarly despite the plants' distinct appearances and distant taxonomic relationship.

We hypothesize that a decline in leaf production is associated with migration away from the Atlantic coast toward the center of the Isthmus of Panama where there is a continuation of leaf flushing. In 1995, leaf production was high on the Atlantic coast

and then declined. Hence, larval crowding or a lack of oviposition sites due to resource limitation may have been a driver for the migration of *M. chiron*. However, leaf production also declined in the center of the isthmus to eventually become less than that on the Atlantic coast. Hence, data from 1995 do not support the hypothesis. In contrast, the El Niño year of 1997 saw a decline in leaf productivity on the Atlantic coast, which may have resulted in local larval crowding and a reduction in suitable oviposition sites prior to the day of the maximum migratory rate. Migrants flew away from the Atlantic coast toward the center of the isthmus where, in that year, there was a continuation of leaf flushing. Hence, data from 1997 do support our hypothesis for a directional migration based on escape from a limited resource. The butterflies may have flown to the dry Pacific coastal forests where we lack information on hostplants for *M. chiron*. Data over a longer term, preferably over a larger spatial scale, are needed to fully evaluate the light limitation hypothesis as a driver of this directional migration.

We have shown that increased primary productivity in wet forests during El Niño years influences herbivore populations across a migratory flyway. The more typical scenario is for the ENSO to affect herbivore populations in subtropical desert and seasonally dry grasslands (Polis *et al.* 1997, Meserve *et al.* 2003, Vandenbosch 2003, Holmgren *et al.* 2006). A pulse of primary productivity with increased rainfall in dry regions, leads to population expansion at higher trophic levels. For rodents, however, Meserve *et al.* (2003) conclude that population control shifts from bottom-up in dry years when resources are limited, to top-down in wetter years. Similarly, Morrison and Bolger (2002) concluded that primary productivity limited breeding success of rufous-crowned sparrows during drier La Niña years, whereas population control shifted to top-down during wetter El Niño years. Although we focus on the effect of changes in hostplant productivity on *M. chiron* abundance, we have little information on how top-down control by parasitoids and predators changes with the ENSO. So, the El Niño migration syndrome in wet and dry tropical forests and subtropical desert and savanna regions may be similar, but the mechanisms may differ in that rainfall in subtropical regions increases during El Niño years whereas it declines in tropical wet forests. Plants respond by producing more leaves that results in a pulse of herbivory, population expansion, and migration. The ENSO cycle not only teleconnects to tropical and subtropical forests but also agricultural systems in many regions of the world (*e.g.*, brown locusts *Locustana pardalina* in southern Africa, Todd *et al.* 2002, leaf-miner flies *Liriomyza* spp. in coastal Peru, Mujica & Kroschel 2011, and brown planthoppers *Nilaparvata lugens* in Southeast Asia, Xiaoqing *et al.* 2007).

The frequency and amplitude of the ENSO cycle will have a strong influence on the frequency and amplitude of insect outbreaks in the future. Although models agree that air temperatures and mean sea surface temperatures will increase in the future, they do not agree that the frequency or amplitude of El Niño events will respond to climate change (Yeh & Kirtman 2007, Collins *et al.* 2010). Over the past 1100 yr, ENSO climate variability was greater in anomalously warmer eastern Pacific conditions

(Li *et al.* 2011), and contemporaneously, an abrupt shift to warmer conditions occurred in 1976 followed by greater interannual variability in the ENSO (Urban *et al.* 2000). Under future climatic projections, uncertainty lies in whether the mean state is toward an El Niño- or La Niña-like future with an El Niño-like state being favored by atmospheric models and a La Niña-like state by oceanic models of circulation (for a detailed discussion, see Coelho & Goddard 2009). Although some circulation models suggest that an El Niño-like mean state is more likely, predictions of precipitation vary much more between sites than projected changes in ambient temperature. The near future promises to bring greater integration of global climate forecasts and ENSO in the next coupled climate comparison project of the World Climate Research Programme (CMIP5, *e.g.*, Kim & Yu 2012, Stevenson *et al.* 2012).

Land-use changes can also alter climate and perhaps influence the ENSO. Climate models indicate that complete tropical deforestation would lead to increased air temperature and surface winds and reduced precipitation locally (Zhang *et al.* 1996a), and would alter atmospheric circulation globally (Zhang *et al.* 1996b). During the last century, lianas have become more abundant in Amazonian and Panamanian wet forests in association with decreasing precipitation (Schnitzer & Bongers 2011). Our data indicate that not only host lianas for *A. statira* but also host trees for *M. chiron* would have also benefitted from this increasing dryness, with the insects increasing in abundance accordingly.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

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

FIGURE S1. Circular diagrams of the mean orientation relative to geographic North and 95% confidence limits for *Marpesia chiron* on the Atlantic coast and the center of the isthmus.

FIGURE S2. The maximum number of *M. chiron* that were counted crossing the transect each day shown for the 17-yr period.

FIGURE S3. Leaf flushing phenology for three hostplants observed in the center of the Isthmus of Panama.

FIGURE S4. Leaf flushing phenology for *Artocarpus altilis* on the Atlantic coast.

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