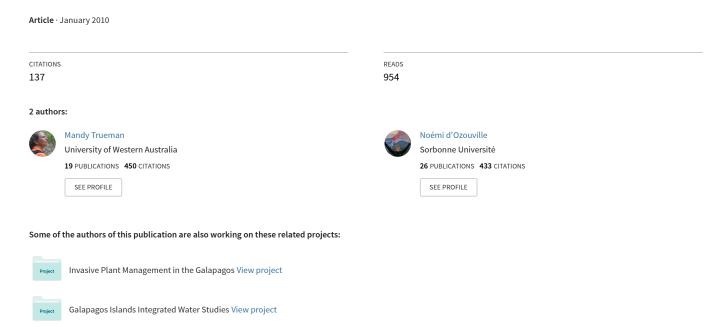
Characterizing the Galapagos terrestrial climate in the face of global climate change



CHARACTERIZING THE GALAPAGOS TERRESTRIAL CLIMATE IN THE FACE OF GLOBAL CLIMATE CHANGE

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SUMMARY

The position of Galapagos in the Eastern Pacific gives it a unique seasonal climate that is atypical of other equatorial oceanic islands. Conditions are influenced by the interaction of ocean currents and winds, governed by the movement of the Inter-Tropical Convergence Zone, and by the periodic Pacific-wide El Niño Southern Oscillation. Weather data from 1959 to 2009 on Santa Cruz Island show that the hot season prevails from January to May, characterized by elevated sea and air temperatures and highly variable rainfall. During the cool season, from June to December, cooler temperatures and a stratus cloud layer persist, resulting in relatively consistent precipitation in the humid highlands and almost none in the dry lowlands. Hot season rainfall totals are strongly correlated with sea surface temperature, whereas cool season rainfall totals are consistent from year to year, and not so closely correlated with sea surface temperature. Seasonal rainfall totals from ten locations on six islands show correlations among the majority of sites for the hot season but fewer for the cool season, one exception being the correlation between sites on Santa Cruz Island, all of which receive at least some cool-season precipitation. Biological productivity in the dry lowlands is primarily influenced by the variable hot-season rainfall. The humid highlands are maintained by more consistent precipitation every year in the cool season, but are also affected by conditions during the hot season. We suggest that the dry zone is vulnerable to a warmer, wetter climate which would favour invasive species and thereby doubly threaten aridadapted endemic species. Potential climate change impacts on the already-invaded and more species-rich humid highlands are harder to predict due to our lack of understanding of cool-season precipitation patterns. In order to understand spatial climate variability in Galapagos better, there remains a need for meteorological data with a greater spatial spread throughout the islands, especially at higher altitudes.

RESUMEN

Describiendo el clima terrestre de Galápagos a la luz del cambio climático global. La posición de Galápagos en el Pacífico del Este le da un clima estacional único atípico en otras islas oceánicas ecuatoriales. Estas condiciones están influenciadas por la interacción entre las corrientes oceánicas y los vientos, regidas por el movimiento de la Zona de Convergencia Intertropical y por el fenómeno periódico a lo largo del Pacífico de El Niño Oscilación del Sur. Datos del clima en la Isla Santa Cruz desde 1959 hasta 2009 muestran que la estación cálida prevalece de Enero a Mayo, caracterizada por temperaturas elevadas del mar y del aire y por alta variabilidad de la precipitación. Durante la estación fría, de Junio a Diciembre, temperaturas más bajas y una capa de nubes estratos persisten, resultando en una precipitación relativamente consistente en las zonas altas húmedas y practicamente ninguna en las zonas bajas secas. La precipitación total de la estación cálida se correlaciona fuertemente con la temperatura de la superfice del mar, mientras que la precipitación total durante la estación fría es consistente de año a año, y no se correlaciona tan cercanamente con la temperatura de la superficie del mar. La precipitación total estacional de diez locaciones en seis islas muestran correlaciones entre la mayoría de los sitios para la estación cálida pero hay menos correlaciones para la estación fría, siendo una excepción la correlación entre sitios en la Isla Santa Cruz, de los cuales todos reciben al menos alguna precipitación de estación fría. La productividad biológica en las zonas bajas secas está primordialmente influida por la precipitación variable de la estación cálida. Las zonas altas húmedas son mantenidas por precipitaciones más consistentes cada año en la estación fría, pero también son afectadas por las condiciones durante la estación cálida. Sugerimos que la zona seca es vulnerable a un clima más caliente y más húmedo, lo cual podría favorecer especies invasoras y por lo tanto amenazar doblemente las especies endémicas adaptadas a las condiciones secas. El impacto potencial del cambio climático en las zonas altas húmedas más ricas en especies y ya invadidas es más difícil de predecir debido a nuestra falta de comprensión de los patrones de precipitación de la estación fría. Para poder comprender mejor la variabilidad climática espacial en Galápagos, queda la necesidad por datos meteorológicos de mayor amplitud espacial a lo largo de las islas, en especial a mayores altitudes.

INTRODUCTION

Located on the equator, 1000 km west of the coast of South America, the Galapagos Islands have a unique climate influenced by the interaction of oceanic currents and winds. Early visitors to the archipelago noted the comparative cool of the climate in comparison with other places on the equator (Dampier 1729, Darwin 1845), the occurrence of two distinct seasons (Dampier 1729), and the presence of a humid "luxuriant vegetation" zone in the uplands, compared to the "sterile" lowlands (Darwin 1845). These features are still the most notable of the Galapagos climate, along with the formidable periodic influence of hot, wet El Niño years and their dry La Niña counterpart (Snell & Rea 1999). With the benefit of modern climatic records a deeper understanding of the Galapagos climate is possible.

Here, we provide a climate analysis preceded by a review of climate reporting and climate mechanisms as contextual information. With current concern for global climate change and its impacts, this knowledge is necessary to predict potential consequences for terrestrial biodiversity in Galapagos. Our analysis incorporates previously unpublished data for the last decade. We use Santa Cruz meteorological data to characterize the climate because it contains continuous and parallel long term data from both lowland and highland sites. We use data from 1959 to 2009 to describe climate features throughout the year and to reveal trends over time. We differentiate two seasons, hot and cool, each of which has distinct influences on biological productivity and hence biodiversity. We also use rainfall data from an additional eight stations on six islands to improve understanding of the spatial distribution of rainfall throughout the archipelago. We discuss potential biodiversity changes in each of the two main climatic zones as a result of global climate change.

GALAPAGOS CLIMATE REVIEW

Climate reporting

Alpert (1946) established the first systematic collection of climatic data on the islands, at a weather station on the island of Baltra during the Second World War. His observations formed the basis of a seminal paper on the climate of Galapagos (Alpert 1963). Palmer & Pyle (1966) wrote about the dry climate of Galapagos in relation to their geographical position and oceanographic conditions. Colinvaux (1968, 1972, 1984) used lake and bog cores to show that the Galapagos climate has been primarily dry for thousands of years, punctuated with some wetter events. This and other palaeoclimatic research has been reviewed by Bush *et al.* (2010).

These early publications contained very little quantitative information (P.R. Grant & Boag 1980) but this changed when Hamann (1979) used data from 14 stations on five islands to construct climatic diagrams and relate

climate to vegetation types. An excellent report on a range of climate measurements from 1964-81 at seven of these stations was presented by Nieuwolt (1991), noting the seasonal climate that is atypical for equatorial locations. Nieuwolt observed the year-round suitability of the highlands for agriculture but acknowledged that rainfall irregularity is a limiting factor in the hot season. The most comprehensive analysis of the existing weather data was carried out by Huttel (1995), including data from some of the same stations as Hamann, for a total of 14 stations on six islands, all registered with the national meteorological institute (INAMHI) network but most of them no longer in operation, and from temporal subsets of the period 1950–87. Huttel (1995) identified three rainfall "vectors" for coastal, transition and highland zones, and noted the lack of data between the coast and 170 m altitude, and above 600 m. Following the 1997–8 El Niño event, Snell & Rea (1999) analyzed the trends in data from the Charles Darwin Research Station and Bellavista, in relation to the occurrence of El Niño events.

Climate measurements have also been important in other studies, especially in relation to finches (*e.g.* P.R. Grant & Boag 1980, P.R. Grant 1985, P.R. Grant & Grant 1996), vegetation (Hamann 1979, Jäger *et al.* 2009), hydrology (Navarro Latorre *et al.* 1991, d'Ozouville 2007) and natural resource management (d'Ozouville 2008).

Climate mechanisms

The Galapagos climate is controlled by the interaction of oceanic currents that surround the islands and the predominant trade winds from the southeast. The influence of the currents and winds is governed on an intra-annual basis by the north-south migration of the Inter-Tropical Convergence Zone (ITCZ), a warm band of deep convection that shifts from 10°N during the northern hemisphere summer to 3°N during the northern winter (Sachs et al. 2009). For the majority of the year the ITCZ is well north of Galapagos, and the southeast trade winds blow across Galapagos, bringing with them air cooled by the cold, upwelled waters to the south (Alpert 1946, Colinvaux 1984). When the ITCZ migrates southward, closer to Galapagos, the archipelago is almost in the doldrums; the trade winds are reduced, warmer ocean currents from the north arrive, and conditions in the archipelago are tropical (Alpert 1946).

This intra-annual ITCZ migration gives rise to the two seasons which characterize the Galapagos climate: a hot season and a cool season (Hamann 1979, Itow 2003). These seasons have in the past been referred to as wet and dry respectively (e.g. Alpert 1946, Palmer & Pyle 1966, Colinvaux & Schofield 1976, P.R. Grant & Boag 1980), as the vast dry lowlands of the archipelago only receive substantial rain in the hot season (except in El Niño years). The wet/dry nomenclature can however be misleading, because the highlands of the islands are typically wetter during the cool season (Hamann 1979) and the lowlands can also be very dry during the hot season. The hot season

is characterized by convection, resulting in orographic rainfall that increases with altitude (Snell & Rea 1999). The cool season is characterized by an inversion layer, when air cooled by the ocean surface is trapped below warmer air, creating condensation just below where the two air masses meet (Colinvaux 1984), especially on the windward side of the islands where air is pushed up against the land (Hamann 1979) (Figs 1 &2). This condensation usually occurs above 250 m altitude and creates extensive stratus clouds, often down to ground-level, locally called garúa (Hamann 1979, Colinvaux 1984, Nieuwolt 1991). These clouds result in two forms of precipitation; vertical (rainfall) and occult, the latter consisting of fog that condenses on vegetation and drips or runs down to the ground. In Galapagos, occult precipitation can significantly increase the total precipitation amount under dense vegetation (Jäger et al. 2009). Data used in this analysis do not include occult precipitation because the rain gauges are not situated beneath vegetation.

A Pacific-wide phenomenon also plays an important role in Galapagos climate: El Niño Southern Oscillation (ENSO). The warm phase of ENSO is referred to as El Niño and the cold phase as La Niña. During El Niño events the eastern Pacific experiences high sea surface temperature, weakening of the southeast trade winds and deepening of the thermocline; all of which strengthen conditions associated with the southward displacement of the ITCZ. The effects in Galapagos include high air temperatures, torrential rainfall and a longer than usual hot season (Snell & Rea 1999). La Niña events bring colder than normal conditions and drought, although the effects of ENSO on cool season climate dynamics are not well understood (Sachs & Ladd 2010). Palaeoclimatologists have used coral cores and lake or bog sediments to show that ENSO fluctuations have been occurring in the archipelago for hundreds to thousands of years (Dunbar et al. 1994, Riedinger et al. 2002, Conroy et al. 2009).

ENSO events (or years) have been defined in many different ways that include either or both atmospheric and oceanographic indices (e.g. Smith & Sardeshmukh 2000). Consequently, lists of events are not consistent with each other or for different regions, nor with effects experienced in Galapagos, especially for less intense events. Also, there are inconsistencies in the listing of years in which events occurred because some El Niño events persist for two consecutive hot seasons, with a cool season in between, while others begin in November or December and extend through a wet season until June the following year. Recent El Niño events in Galapagos include 1975-6, 1982-3, 1986-7, 1993-4 and 1997-8 (Snell & Rea 1999). The very strong events of 1982–3 and 1997–8 had dramatic effects on Galapagos ecosystems (Robinson & del Pino 1985, Snell & Rea 1999, Vargas et al. 2006). Within the last decade, El Niño events have caused high rainfall in the hot seasons of 2002 and 2010. High rainfall in 2008 was not associated with an El Niño event.

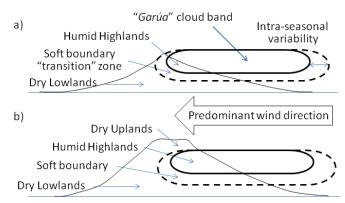


Figure 1. Galapagos landscapes with cool-season cloud and the resulting climatic zonation: a) islands of intermediate height (Santa Cruz, San Cristóbal, Floreana, Santiago, Pinzón, Pinta); b) the six volcanoes of Isabela and Fernandina islands.

Climate zones

The stratus cloud layer that dominates each cool season has led to a climatic zonation from the dry lowlands to the humid highlands, and on the higher islands to a third zone, the dry uplands (Fig. 1). Whilst these climatic zones have not been mapped, they correspond to naturally occurring semi-arid and humid vegetation zones as described by Hamann (1979) and mapped by Huttel (1986) (Fig. 3). We refer to these as climatic zones rather than vegetation zones, partly because the natural vegetation zonation is more complex and is a response to these climatic factors, and partly because the natural vegetation zonation has been completely altered by anthropogenic change on the inhabited islands (Snell *et al.* 2002, Watson *et al.* 2009), whilst the climatic drivers have generally been maintained.

The soft boundary between the humid and dry climatic zones (Fig. 1) matches the vegetation "Transition Zone" of Wiggins & Porter (1971) (Fig. 3), which has been characterized in terms of climate and vegetation (see also



Figure 2. Satellite imagery showing typical cool-season stratus cloud formation over central-west Galapagos on 25 Nov 2009. Source: Landsat 5, USGS http://edcsns17.cr.usgs.gov/cgibin/EarthExplorer.

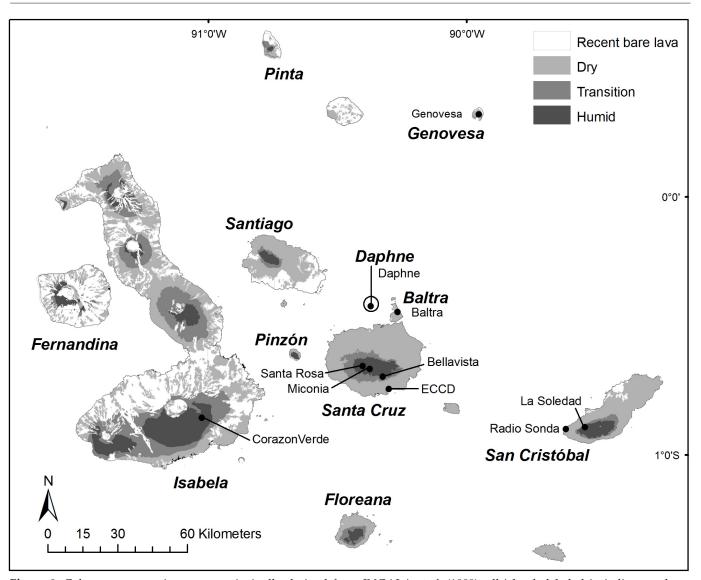


Figure 3. Galapagos vegetation zones, principally derived from INGALA *et al.* (1989), all islands labeled in italics are those referred to in this paper, and all sites labeled in smaller lettering are those with meteorological data used in this paper.

Hamann 1979, Mueller-Dombois & Fosberg 1998, Itow 2003). The dry zone on the tops of the higher volcanoes (Cerro Azul, Sierra Negra, Alcedo, Darwin, Wolf and Fernandina) which extend above the upper limit of the stratus cloud (Fig. 2), has not been fully described in terms of vegetation or climate, but has been recognised in climate discussions (Colinvaux 1984) and vegetation descriptions (Porter 1979, van der Werff 1978, Weber & Gradstein 1984). It was mapped by Huttel (1986) using satellite imagery, where it corresponds to the calderas of Sierra Negra, Darwin, Wolf and Fernandina volcanoes. Such a zone has been described in other volcanic islands, such as La Réunion (Barcelo & Coudray 1996), in relation to rainfall.

The location of the windward, and hence more humid, side is not consistent among all islands and volcanoes (Figs 1–3). Although the prevailing winds in the archipelago come from the southeast, it appears that wind

direction is altered in the lee of other islands or volcanoes. This is especially apparent on the large volcanoes of Isabela and Fernandina islands, where the humid highlands occur on either the southern or western side of the various volcanoes. Mapping and defining these zones in relation to cloud cover, rainfall, occult precipitation and wind would aid our understanding of local climate mechanisms, especially in relation to *garúa*. Sachs & Ladd (2010) identify this topic as important for understanding potential climate change impacts in Galapagos.

ANALYSIS

Methods

We characterize the climatic conditions based on data from the two main meteorological stations on Santa Cruz Island: ECCD (0°44′37.6′′S, 90°50′21.9′′W) at 2 m a.s.l. at the Charles Darwin Research Station near Puerto Ayora,

and Bellavista (0°41′46.53′′S, 90°19′37.20′′W) at 194 m a.s.l. (Fig. 3). Many of the data used here are available for download at <www.darwinfoundation.org>. These locations are used to represent the dry lowlands and the humid highlands respectively, although each is located at the lower altitudinal limit of these two climatic zones respectively.

To understand temporal variation within years, we describe the annual variation in key climate variables by charting monthly averages using available data for the two stations. The variables used are sea surface temperature (SST), total rainfall, number of rain days (defined as days where rainfall >0), air temperature, humidity, sunshine hours and wind (strength and direction). For rainfall and rain days we used median instead of mean, as recommended by Nieuwolt (1991), due to the highly skewed variation in rainfall in many months. All data were collected daily, and were summarized into charts of monthly averages or totals using Microsoft Excel.

For SST, the variation in recordings for each month is indicated by standard deviation, and for rainfall by the interquartile range. Seasonal trends in other climate variables are not presented here as they did not show any distinct patterns. No different treatment was carried out for El Niño years.

At each station, data were collected on different climatic variables and over different periods. At ECCD data on most variables were available from January 1965 to October 2009, except sunshine hours, which began in January 1978, and wind, which began in July 1987 and terminated in July 2009. At Bellavista, data on most variables were available from July 1987 to September 2009, except sunshine hours, which began in April 1994. Some daily data are missing for wind and sunshine at both locations. SST was recorded at the coast in a bucket of water pulled from the sea. Air temperature was recorded in shade 2 m above the ground; we use daily minimum and maximum. Daily rainfall is the sum of measurements taken at 12h00, 18h00 and 6h00 the following day, in a rain gauge 1.5 m above the ground. All data were recorded manually.

To define the general timing of seasons we determined in which month each season had begun for all years 1965–2009, using SST. We defined the transition between hot and cool seasons as the month in which the mean SST reached the midpoint between the highest (or lowest) monthly mean SST of the hot (or cool) season and the subsequent lowest (or highest) monthly mean SST of the following cool (or hot) season. From this we determined the season in which each month most frequently occurred, and therefore a predominant annual pattern of the seasons.

We summed rainfall data and averaged SST for each seasonal period (hot = January–May, cool = June–December) and over the whole year, each year, at ECCD and Bellavista. The seasonal SST averages and rainfall totals were plotted as time series to assess trends, and the

rainfall totals were also used to compute the median, minimum and maximum seasonal and annual rainfall at the two stations, identifying in which season the larger proportion of the rainfall fell at each. We also tested for a correlation between seasonal and annual rainfall totals and SST averages. We identified four "outlier" years, of exceptional rainfall in the cool season: all years in which El Niño events extended into the normal cool season months (1972, 1982, 1983 and 1997). These years are unrepresentative of cool season rainfall and were therefore excluded from some analyses, as mentioned below. Although hot season rainfall totals were also exceptional in El Niño years, none of these are considered outliers because they form part of a continuous trend of hot season rainfall in relation to SST (see below, Fig. 6).

To understand the spatial variation of rainfall across the archipelago, we used data from an additional eight locations with records from a minimum of six years. These sites (and the years of available data) are: Baltra (1999–2008), Corazon Verde (1970–99 except 1974 and 1995), Daphne (1976-2008), Genovesa (1978-88), La Soledad (1997–2007), Miconia (1996–2005), Radio Sonda (1977-83; 2002-8), and Santa Rosa (2003-8) (Fig. 3). These stations represent six islands, with half of the sites located in the humid or transition zone and the other half in the dry zone. Most data were provided as daily rainfall totals by the Charles Darwin Research Station. Data from Genovesa were obtained from B.R. Grant & Grant (1989) in monthly totals for January-May in all years except 1982-3 (Jan-May 1982 and December 1982 to July 1983). Daphne data were provided by P. & R. Grant (pers. comm.) as annual totals, but are interpreted here as hot season rainfall only, because cool season rainfall on that island is negligible (P. Grant pers. comm.).

Rainfall data were summed to produce seasonal totals for each of the ten locations, using the above-defined periods for the seasons. To examine matches between locations for each of the hot and cool seasons, data were plotted as time series. Correlation coefficients were generated (in Microsoft Excel) to compare rainfall at each location with each of the other locations, for all pairs of data sets which had at least five years of concurrent data. For the cool season, four outlier years were excluded, as explained above. To understand spatial variation within a single island, some daily rainfall data of extreme rainfall events were compared between ECCD in the lowlands and Bellavista in the highlands.

Rainfall isohyets were created for each of the hot and cool seasons for Santa Cruz Island, using rainfall records for the four stations on this island plus those on Daphne and Baltra, along with data from three additional highland sites on Santa Cruz (S. Henderson pers. comm., d'Ozouville 2007, Jäger et al. 2009) and existing vegetation mapping (INGALA et al. 1989). We performed a manual interpolation of median seasonal rainfall totals, guided by vegetation zone boundaries and altitude.

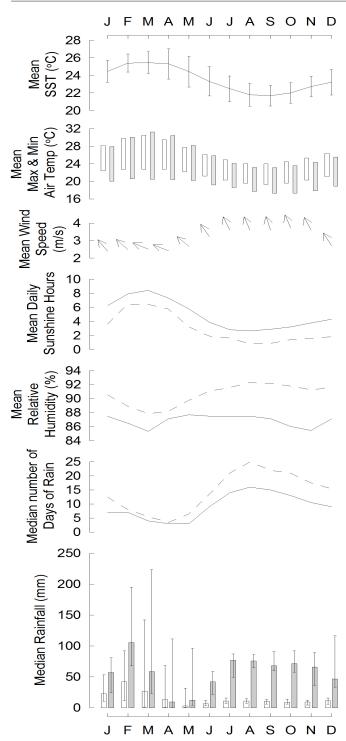


Figure 4. Annual variation in climate variables in Galapagos over the period of data availability. SST are expressed as monthly means \pm S.D., recorded at ECCD. Monthly air temperature bars indicate mean daily minimum and maximum for ECCD (white) and Bellavista (grey). Wind speed is the monthly mean (base of arrow) of daily records at ECCD (median of 24 measurements per day), with arrows showing mean direction for each month. Sunshine and humidity are expressed as monthly means of daily records, and number of rain days as the median of all years, for ECCD (solid line) and Bellavista (dotted line). Rainfall bars show median monthly totals for ECCD (white) and Bellavista (grey), with error bars depicting the interquartile range.

Results

Defining the seasons. Data from ECCD and Bellavista show two distinct periods of the year, hot and cool, driven by sea surface temperatures that were higher in the first half of the year (Fig. 4). The hot season generally began in January, peaked in February and March, and finished in May (Fig. 5). However, it occasionally started as early as November or finished as late as July. The cool season thus generally began in June, peaked in August–October and finished in December (Fig. 5). Occasionally, it started as early as April and finished as late as the following January. For the analyses below, we define the seasons as January–May for the hot season, and June–December for the cool season.

Annual variation at ECCD and Bellavista. Air temperatures were also higher in the hot season than in the cool season. Daily maxima were generally 5°C warmer than the minima, except in the sunnier months of February–April when daytime maxima were an additional 3–9°C higher. In general, temperatures at Bellavista were lower than at ECCD, with daily minima being usually 2°C lower in most months of the year. Only during the hot season months of February–May were average daily maxima about 1°C higher in Bellavista than at ECCD.

During the hot season, daily median wind speed averaged *c*. 2.4 m.s⁻¹ and wind direction was very variable. In the cool season, daily median speed averaged highest (3.7 m.s⁻¹) in October and winds came from the south-southeast with little variability.

Sunshine hours per day were greater during the hot season than the cool season. More sunshine hours were registered at ECCD than at Bellavista throughout the year.

Humidity was consistently high throughout the year in both stations, but dropped slightly in March–April, and at ECCD again in November.

Rainfall was extremely variable in the hot season at both stations. Peak median rainfall occurred in February in both locations, although zero monthly rainfall was sometimes experienced at ECCD during February–June, and in Bellavista from March to May. Rainfall in Bellavista was higher than ECCD throughout the year, but particularly in the cool season, when Bellavista received *c*. 70 mm

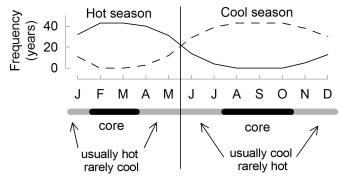


Figure 5. Frequency of the Galapagos hot and cool seasons occurring in each month of the year, based on SST.

per month and ECCD *c.* 10 mm per month. In the cool season, the amount of rainfall was fairly consistent from month to month and year to year.

At both stations, the median number of rain days per month was lower in the hot season than in the cool season. The peak month for rain days at both locations was August. The month with fewest rain days was May at ECCD, April at Bellavista. Number of rain days was not closely related to the amount of rainfall. Rain days at ECCD during the cool season typically produced < 2 mm of precipitation (>80 % of records), but rain days in the hot season often produced > 5 mm (> 40 % of records), and sometimes considerably more: there are ten records of days with>100 mm of rainfall at ECCD, all in the hot season.

Median annual rainfall was three times higher in Bellavista than at ECCD (Table 1). At ECCD, the majority of the median annual rainfall occurred in the hot season (Table 1). In very dry years, hot-season rainfall was far below the median and often far below the usual hot-season proportion of the annual total; for example, in 1985 only 5 mm of rain was recorded during the hot season at ECCD, out of a total of 64 mm that year. Conversely in Bellavista, more of the annual precipitation occurred in the cool season (Table 1).

Rainfall at ECCD and Bellavista was significantly positively correlated with SST in the hot season, with no obvious outlier years (r = 0.86 and 0.82 respectively; P <0.001; Fig. 6a). In the cool season, there was a weaker correlation at both locations (r = 0.65 and 0.78 respectively; P < 0.001) and when we excluded the obvious cool-season outlier years (1972, 1982, 1983 and 1997), that corresponded to El Niño events in which hot season conditions extended into normally cool-season months, the correlation was further weakened, though still significant (r =0.48 and 0.45, P = 0.002 and 0.040 respectively; Fig. 6b). Trends at ECCD. The ECCD time series of monthly rainfall and SST from 1965 showed the high variability of rainfall in the lowland zone, with periods of high rainfall corresponding to sustained high SST (Fig. 7). Obvious peaks in hot season rainfall coincided with years of high SST, especially 1983 and 1998 (two extreme El Niño events), when rainfall was high and sustained over many months.

Table 1. Summary rainfall statistics (mm) for ECCD and Bellavista (extreme years given in parentheses).

| | | ECCD | Bellavista |
|-------------|---------|------------------|--------------------------|
| Annual | median | 277 | 813 |
| | minimum | 64 (1985) | 448 (1988) |
| | maximum | 2769 (1983) | 2666 (1997) ¹ |
| Hot season | median | 196 ² | 351 |
| Cool season | median | 81 | 462^{3} |

¹ Bellavista records began in 1988; rainfall might have been higher in the El Niño year of 1983.

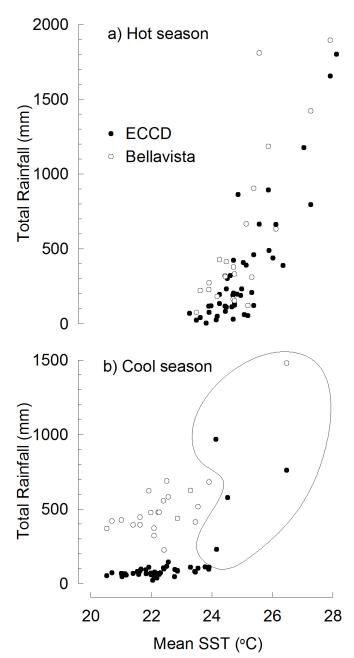


Figure 6. Scatter plot of SST and rainfall in each season at two locations. Obvious outlier years here (circled) are associated with El Niño events that extended into the normal cool season months in 1972, 1982, 1983 and 1997.

Spatial variation. Seasonal rainfall totals appeared to show similar year-to-year patterns at all recording stations in both seasons (Fig. 8). For the hot season, whole-season rainfall at most stations correlated strongly and significantly with most others. Correlation coefficients > 0.77 (P<0.05) existed for 29 out of 35 possible station pairs (83 %), with most (19) of these very strong (r>0.97, P<0.001). The exceptions were: Miconia not correlated with Baltra, and Santa Rosa not correlated with any other site except Radio Sonda, perhaps due to the shorter time-span of the Santa Rosa dataset (n = 6; all others n > 9). For the cool season,

²71% of annual.

³ 57% of annual.

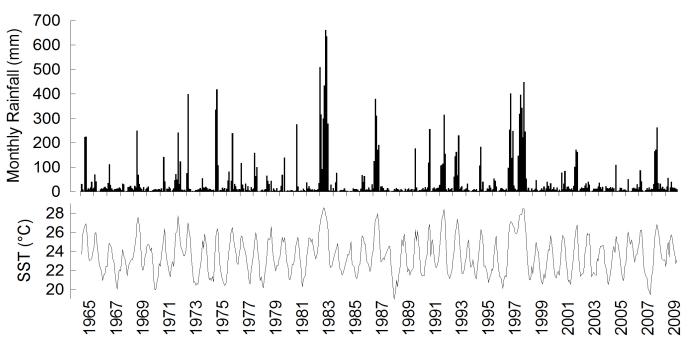


Figure 7. Trends in rainfall (monthly totals) and SST (monthly means) at ECCD, since records began in January 1965 until December 2008.

with the four outlier years excluded, there were fewer correlations among sites. Only nine pairs of 21 possible combinations (43 %) were correlated (r > 0.44; P < 0.05), including sites on Santa Cruz Island (Bellavista correlated with ECCD, Santa Rosa and Miconia; ECCD correlated with Santa Rosa). Also, Radio Sonda correlated with ECCD, Bellavista, Santa Rosa and Baltra, while Corazon Verde correlated with ECCD. Thus, in the cool season, correlations appear to exist mainly within a single island, or perhaps where concurrent datasets span longer periods.

Rainfall during the hot season, whilst correlated among locations for the seasonal totals, was localized in terms of individual events. This is illustrated by the rainfall during 2008, a year in which the SST was relatively normal, yet Bellavista received 1808 mm (Fig. 6a). This exceptionally high total was due to the three days of highest rainfall on record at Bellavista: 7, 8 and 12 March, with 224, 280 and 490 mm respectively (total 994 mm). On those days, rainfall at ECCD was unexceptional (5, 12, and 0 mm respectively), whereas high rainfall was experienced

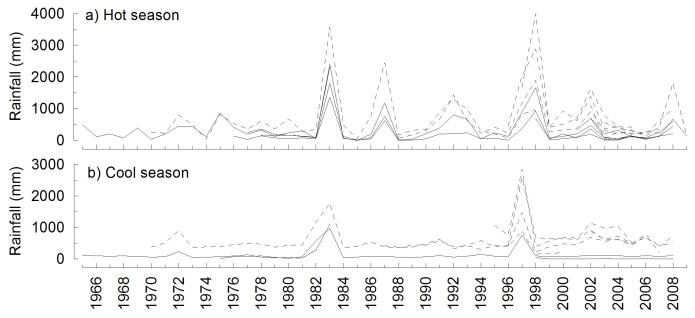


Figure 8. Seasonal trends in total rainfall at lowland (solid lines) and highland (dotted lines) sites for the hot and cool seasons.

on 9 March (55 mm), 3 April (94mm) and 16 April (62mm), when rainfall in Bellavista was 6, 74, and 21 mm respectively.

Isohyet maps (Fig. 9) for Santa Cruz Island show increasing rainfall with altitude in both seasons. Although constructed from limited data, this representation improves on previous maps (Navarro Latorre *et al.* 1991, d'Ozouville 2007). Further improvement should take into account occult precipitation during the cool season, and a greater spatial spread of rainfall recordings.

DISCUSSION

Synthesis

The local oceanic and atmospheric conditions result in two distinct annual seasons in Galapagos, which is atypical of equatorial locations (Nieuwolt 1991). During January to May, when the ITCZ is at its southern limit, close to Galapagos, hot conditions prevail. SST and air temperatures are at their annual peak, winds are mild and predominantly from the ESE (although direction is variable), and most days are sunny (Fig. 4). Rainfall is convective and highly variable, with recorded monthly totals from 0-660 mm at ECCD in the lowlands, and 0-1263 mm at Bellavista in the highlands. Convective storms are often small and short, missing one area while deluging another nearby. Rainfall totals are strongly positively correlated with average SST in the hot season, and also among sites throughout the archipelago. From June to December, when the ITCZ lies further north, cooler conditions predominate, with consistent, cool, southeast trade winds, lower SSTs and air temperatures, and persistent stratus clouds (garúa) (Fig. 2) that wet the highlands while the lowlands remain dry. Rainfall in the cool season is more consistent from year to year and month to month, with monthly totals of around 10 mm at ECCD in the lowlands and 67 mm at Bellavista in the highlands, where it rains almost every day. Total rainfall is only weakly correlated with average SST for the cool season, and there are fewer correlations among sites throughout the archipelago.

ENSO events can alter the length and intensity of the seasons; in particular El Niño events lengthen and intensify the hot season, sometimes to the previous November or December or extending into June or July. This can upset cool season trends, and years identified as cool season outliers (1972, 1982, 1983, 1997) all match El Niño events as defined by Smith & Sardeshmukh (2000).

No obvious long-term trends in SST or rainfall are apparent during the period 1965-2009, which might be expected to be associated with global climate change. This may be partly due to the strength of ENSO influence, which provides so much noise that it potentially obscures signal. Records for this period show a significant positive correlation between SST and rainfall, although this is only strong in the hot season. A correlation of rainfall with SST in Galapagos has previously been noted (Houvenaghel 1974), presumably using annual rainfall totals from coastal data, where cool season rainfall contributes little to annual totals. Our findings that, apart from major El Niño years, cool season rainfall is consistent from year to year, only weakly correlated with SST and not correlated between locations except within the highland zone of a single island, beg questions about the drivers of the cool season garúa (see also Bush et al., Sachs & Ladd 2010).

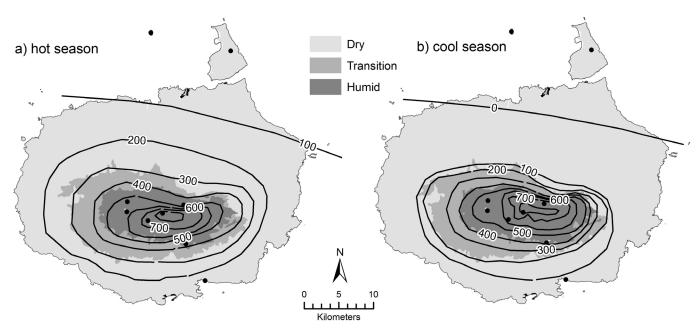


Figure 9. Isohyets for total seasonal rainfall on Santa Cruz Island (mm) for the (a) hot season and (b) cool season. Dots indicate the locations of stations whose data was used to develop these isohyets.

Differences in all climate variables are apparent between the lowlands and highlands. Rainfall is greater in the highlands throughout the year, and this difference is most pronounced during the cool season when rainfall in the lowlands is minimal. However, rainfall is likely to decrease above 800 m, at least in the cool season when the stratus cloud lies below this altitude, which accounts for the presence of a further dry zone on the tops of the higher volcanoes (Huttel 1986). We do not know of any rainfall measurements in this dry upland zone. The decreasing temperature gradient from the lowlands to the highlands is consistent with the results of d'Ozouville (2007), who calculated an average gradient throughout the year of −0.8°C per 100 m altitude on Santa Cruz from 0–855 m. This is steeper than the c. -0.5°C per 100 m gradient expected in the humid tropics due to the adiabatic lapse rate (Bush & Silman 2004). Considering that the highlands receive < 3 h of sunshine per day in the cool season and < 6 h per day in the hot season, there may be a significant cooling effect from cloud-shadow in the highlands, especially during the cool season. The slightly higher maximum temperatures in Bellavista compared to ECCD during the hot months of February–May are not consistent with the annual means or with expected adiabatic lapse rates. Whilst our results do not suggest any clear causation, we propose that this may be due to the cooling effect of the ocean on ECCD temperatures, as this station is situated only 20 m from the sea.

While monthly rainfall totals are variable between locations in Galapagos, as observed by Nieuwolt (1991), we show that hot season rainfall totals are correlated among locations throughout the archipelago. Whilst cool season rainfall appears to be relatively constant from year to year in all locations, it is largely not correlated among locations. Notable exceptions are the correlations between sites within Santa Cruz Island, perhaps suggesting an influence of individual island topography on cool season precipitation.

Climate change

Precipitation is recognized as the primary driver of terrestrial biological productivity in Galapagos (Nieuwolt 1991), so changes to it could induce changes in native species distributions and agricultural productivity. The local effects of global climate change may influence precipitation amount, periodicity, and intensity. Given the varying climate mechanisms at work in Galapagos, the effects are likely to be different in each season (Table 2).

Given our understanding of the Galapagos seasons and their manifestations in the lowland and highland zones, we know that the unpredictable hot season rainfall is important for lowland productivity (Porter 1979), and consistent cool season garúa precipitation is the major driver of productivity in the humid highlands. Therefore, the two broad climatic zones in Galapagos will likely not respond similarly to global climate change, inducing a new source of heterogeneity that may or may not favour the continued existence of vulnerable organisms. The large lowland zone, with its peculiarly dry conditions punctuated by very wet El Niño events, is home to most of the archipelago's endemic plant species (67 %: Porter 1979), many of which are already threatened (Tye 2008). In contrast, the smaller, wetter highland zone hosts the majority of the invasive plants in the archipelago and is already severely affected by past land-use change (Snell et al. 2002, Watson et al. 2009). Some of the potential consequences of altered seasonality are elaborated below.

Local warming and resultant increased hot-season rainfall would probably decrease soil-moisture deficits in the lowlands, thereby reducing the competitive advantage of the characteristic arid-adapted species. This effect has been observed in the short term following El Niño events, when fast-growing species thrive and grow over longer-lived species (Hamann 1985, Tye & Aldaz 1999). If conditions were permanently less extreme, the lowlands would also be more vulnerable to invasion by introduced species, which would be expected to spread from the coastal towns, where many potentially invasive species are currently cultivated in gardens (Atkinson et al. in press). Alternatively, if the hot seasons become drier, some species may not regenerate from soil seed banks. The importance of these seed banks to demography of some species has been suggested based on the mass germination and replenishment of their soil seed banks after El Niño rains, in places or islands where they had not been recorded before (Luong & Toro 1985, Trillmich 1991).

It is harder to say what the impacts might be in the humid highlands because changes to cool season precipitation are harder to predict, given a lack of understanding of their drivers (Sachs & Ladd 2010). It has been proposed that the cool season *garúa* has been prevalent in Galapagos for at least the last 48,000 years (Colinvaux 1972), so the biota are long adapted to this regime, so any reduction in *garúa* formation could be catastrophic for natural ecosystems. It is unclear if *garúa* would cease to form if SST were to remain above a certain level, so this is an important

Table 2. Possible effects of global climate change on Galapagos climate, by season.

| Possible changes | Hot season | Cool season |
|--------------------|--------------------------------|--|
| Trend Warmer | More convective rain, warmer. | Unknown changes to precipitation, cloud cover, humidity, wind. |
| Cooler | Less convective rain, cooler. | Unknown changes to precipitation, cloud cover, humidity, wind. |
| ENSO More frequent | More high-rainfall years. | Shorter cool seasons. |
| More intense | More years like 1983 and 1997. | More years like 1983 and 1997. |

area of future research. Changes to the hot season would likely also have impacts in this zone, although, using El Niño events as a guide, changes in productivity are not as pronounced there as in the dry zone (Hamann 1985, Luong & Toro 1985). However, one possible outcome of increased frequency of El Niño events is further damage to the highland Scalesia woodlands, which have already been reduced to 1.1 % of their original size on Santa Cruz (Mauchamp & Atkinson in press). This genus has suffered from mass dieback during some of the major previous El Niño events (Hamann 1985, Tye & Aldaz 1999), and impacts could be much worse now, with the increased presence of invasive plants in this community (see Mauchamp & Atkinson in press). Any such impacts would add to the already extensive degradation of the highlands.

Data needs

Despite early recognition that meteorological data were lacking for large parts of the archipelago (Alpert 1963, Hamann 1979), including the high-altitude dry zone, these data are still lacking. In particular, finer-scale data are needed, with greater spatial coverage, especially on the uninhabited islands and at higher altitudes. These would help elucidate local climate processes and their linkage with biological productivity; thereby increasing our ability to predict climate change impacts. Most of the long-term records are from coastal locations (P.R. Grant & Boag 1980), yet recent research highlights the need to understand highland processes (Bush et al. 2010). Some data from highland weather stations and rain gauges from S. Henderson (unpubl.), d'Ozouville (2007), Jäger et al. (2009) and M. Bush (unpubl.) provide interesting results but there has been no long-term monitoring. In particular Jäger et al. (2009) highlight the importance of interception of garúa by vegetation in the highland zone, paving the way for further research in that field. Also, d'Ozouville (2007) showed the importance of cool season precipitation for the recharge of the hydrological system. Satellite data may contribute to an archipelago-wide climate model, but need to be supplemented with groundbased measurements at more localities. Climate data are currently dispersed among institutions and individuals, making it challenging to collate information for an archipelago-wide understanding. When comparing rainfall data from automatic rain gauges with those from manual stations (ECCD, Bellavista, Puerto Baquerizo Moreno) and the national climate network (INAMHI), daily totals should be summed from the first time-step after 6h00 until 6h00 of the following day (see Methods, above). All data could be centralized and made available on the internet, perhaps alongside the data from ECCD and Bellavista at <www.darwinfoundation.org>. The Galapagos National Park Service could establish weather stations in more isolated sections of the archipelago, while visiting scientists with projects requiring climatic data should be encouraged to contribute data, and perhaps to help expand a long-term climate monitoring network over the islands.

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