Journal of Biogeography (*J. Biogeogr.*) (2007) **34**, 1357–1373

SPECIAL ISSUE

Dry spots and wet spots in the Andean hotspot

Timothy J. Killeen[1]*, Michael Douglas[2], Trisha Consiglio[3], Peter M. Jørgensen[3] and John Mejia[4]

[1]*Centre for Applied Biodiversity Science at Conservation International, 1919 M Street NW, Washington, DC 20036, USA,* [2]*National Severe Storms Laboratory/NOAA, National Weather Center, 120 David L. Boren Blvd, OK 73072, USA,* [3]*Missouri Botanical Garden, PO Box 299, St Louis, MO 63166-0299, USA and* [4]*CIMMS/NOAA-Univ. of Oklahoma, National Weather Center, 120 David L. Boren Blvd, OK 73072, USA*

ABSTRACT

Aim To explain the relationship between topography, prevailing winds and precipitation in order to identify regions with contrasting precipitation regimes and then compare floristic similarity among regions in the context of climate change.

Location Eastern slope of the tropical Andes, South America.

Methods We used information sources in the public domain to identify the relationship between geology, topography, prevailing wind patterns and precipitation. Areas with contrasting precipitation regimes were identified and compared for their floristic similarity.

Results We identify spatially separate super-humid, humid and relatively dry regions on the eastern slope of the Andes and show how they are formed by the interaction of prevailing winds, diurnally varying atmospheric circulations and the local topography of the Andes. One key aspect related to the formation of these climatically distinct regions is the South American low-level jet (SALLJ), a relatively steady wind gyre that flows pole-ward along the eastern slopes of the Andes and is part of the gyre associated with the Atlantic trade winds that cross the Amazon Basin. The strongest winds of the SALLJ occur near the 'elbow of the Andes' at 18° S. Super-humid regions with mean annual precipitation greater than 3500 mm, are associated with a 'favourable' combination of topography, wind-flow orientation and local air circulation that favours ascent at certain hours of the day. Much drier regions, with mean annual precipitation less than 1500 mm, are associated with 'unfavourable' topographic orientation with respect to the mean winds and areas of reduced cloudiness produced by local breezes that moderate the cloudiness. We show the distribution of satellite-estimated frequency of cloudiness and offer hypotheses to explain the occurrence of these patterns and to explain regions of anomalously low precipitation in Bolivia and northern Peru. Floristic analysis shows that overall similarity among all circumscribed regions of this study is low; however, similarity among super-humid and humid regions is greater when compared with similarity among dry regions. Spatially separate areas with humid and super-humid precipitation regimes show similarity gradients that are correlated with latitude (proximity) and precipitation.

Main conclusions The distribution of precipitation on the eastern slope of the Andes is not simply correlated with latitude, as is often assumed, but is the result of the interplay between wind and topography. Understanding the phenomena responsible for producing the observed precipitation patterns is important for mapping and modelling biodiversity, as well as for interpreting both past and future climate scenarios and the impact of climate change on biodiversity. Super-humid and dry regions have topographic characteristics that contribute to local

*Correspondence: Timothy J. Killeen, Centre for Applied Biodiversity Science at Conservation International, 1919 M Street NW, Washington, DC 20036, USA.
E-mail: t.killeen@conservation.org

www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2006.01682.x

climatic stability and may represent ancestral refugia for biodiversity; these regions are a conservation priority due to their unique climatic characteristics and the biodiversity associated with those characteristics.

Keywords

Biodiversity, conservation biogeography, dry forest, latitudinal diversity gradients, Pleistocene refugia, precipitation patterns, rain forest, tropical Andes, water-energy dynamics.

INTRODUCTION

The tropical Andes hotspot is the most biologically rich region of the planet (Myers *et al.*, 2000) and the most biologically diverse areas within this hotspot are the eastern slopes where humid air masses from the Amazon impinge the topographic barrier of the Andean Cordillera. The traditional view of the eastern slope is of rain and cloud forests that stretch from Colombia to Argentina, with precipitation decreasing and seasonality increasing with distance from the equator. Species diversity in the Amazon and Andes is assumed to decrease with increasing latitude and most systematic and biogeographical research supports that hypothesis (Cardillo *et al.*, 2005; ter Steege *et al.*, 2006). However, latitude *per se* is not a mechanism for predicting species diversity, and different abiotic and biotic mechanisms have been proposed to explain the observed phenomenon (Hutchinson, 1959; Rhode, 1992; Gaston, 2000; Whittaker *et al.*, 2001).

Numerous hypotheses have been presented to explain this globally consistent trend. One group of hypotheses is based on the large spatial extent of the tropics and the relationship between species diversity and geographical area (Colwell & Lees, 2000; Rosenzweig, 2003). Another group of hypotheses focus on climate and its impact on organisms and ecosystems (Francis & Currie, 2003). Maximum levels of solar energy and unrestricted availability of water allow tropical ecosystems to attain optimum levels of photosynthesis; higher net primary productivity leads to greater biomass and more individuals per area, which allows for more species to be supported within a landscape or region (Brown, 1984; Currie, 1991; O'Brien, 1998, 2006). The processes of speciation, particularly mutagenesis and selection, are enhanced in the high-energy environments of the tropics, accelerating the creation of new species (Rhode, 1992; Cardillo *et al.*, 2005; Wright *et al.*, 2006). Tropical climates have enjoyed relatively constant conditions over millennia when compared with higher latitudes; climatic stability leads to lower extinction rates, allowing tropical biomes to retain a greater number of species (Gaston & Blackburn, 2000). Nonetheless, the historical importance of Pleistocene and Tertiary climate oscillations on the Andean and Amazonian biota is just beginning to be appreciated (Ricklefs & Schluter, 1993; Rasanen *et al.*, 1995; Bush *et al.*, 2004; Mayle *et al.*, 2004). It is now generally accepted that patterns of biodiversity are explained by multiple phenomena that interact at global, regional and local scales (Gaston, 2000; Whittaker *et al.*, 2001). The topographic and climatic characteristics of the eastern Andes and adjacent piedmont in Ecuador, Peru and Bolivia provide an opportunity to study the interaction of some of these phenomena on the distribution of biodiversity.

Precipitation and seasonality vary considerably in western Amazonia and the adjacent foothills, and several areas of high rainfall exist at a considerable distance from the Equator. Several isolated dry regions exist along the eastern flank due to a variety of topographic phenomena generally assumed to reflect local rain shadows (Humboldt, 1807). This regional variability in climate can be used to evaluate whether observed patterns of biodiversity are a simple function of latitude or the result of a more complex interaction of precipitation, seasonality and topography. This information has practical applications for conservation planning as it can be used to stratify the region in terms of habitat heterogeneity in the context of climate change.

The existence of areas of both high and low rainfall along the eastern Andean slopes has been well known to researchers working with national climate maps (INRENA, 1975; Unzeta, 1975; Montes de Oca, 1997; Brack-Egg & Mendiola, 2000). The advent of geographical information systems (GIS) and the availability of large data sets have facilitated the study of climatic phenomena at the continental scale (Lindsey, 2002), including efforts to document the wind patterns associated with the South American monsoon (Nogués-Paegle *et al.*, 2002; Marengo *et al.*, 2004).

Understanding regional patterns of precipitation is important for conservation science and biogeography for several reasons. After more than 200 years of biological inventory, including a fairly intensive effort over the last 30 years, biodiversity maps of the tropical Andes hotspot remain incomplete. Much of the challenge resides in the very nature of the hotspot, where diversity and endemism are so high that it will require many more decades of intensive collecting to map species distributions reliably. Current information is laden with artefact and many efforts to map and model species diversity and endemism do little more than show collecting density (Nelson *et al.*, 1993). In the few cases where the results are fairly convincing, researchers focused on a restricted area that had been subject to intensive collecting by several collaborating institutions (Jørgensen & León-Yánez, 1999; Valencia *et al.*, 2000; Pittman *et al.*, 2002).

The lack of reliable species data for the tropical Andes and the adjacent, equally poorly sampled region of the western Amazon has led conservation scientists to rely on surrogate data, either in the form of a few well-studied taxa, such as birds (Stotz *et al.*, 1996; Patterson *et al.*, 1998), butterflies (Lamas, 1994), mosses (Churchill *et al.*, 1995) and aroids (Vargas *et al.*, 2004) or more commonly on general descriptions of vegetation types (Hueck & Siebert, 1972; Navarro & Maldonado, 2002; Josse *et al.*, 2003). One of the most widely used systems is based on a subjective classification of geomorphology, vegetation cover, precipitation levels and 'expert knowledge' (Olson & Dinerstein, 1998). While improving biological inventory data is a top priority, conservation planners must continue to rely on surrogate data to develop conservation strategies. Data about environmental phenomena are especially important because they can be used not only to characterize regions but also to improve and refine models that propose to depict species ranges based on existing observational data and the environmental parameters associated with these data (Stockwell & Peters, 1999).

One incentive for refining species distribution models is to predict the impact of climate change on species ranges; the goal is to identify species that face the greatest risk over the short or medium term. However, interpreting how climate change might impact upon a species requires an understanding of regional weather patterns, particularly where topography or edaphic phenomena constrain ecosystem function and species distributions. Global change will be manifest not just by shifts in temperatures but also by changes to wind and ocean currents, precipitation patterns and cloud formation (Cox *et al.*, 2000; Houghton *et al.*, 2001). Such basic changes will probably be amplified by altered land use, simplification of habitat structure (Shukla *et al.*, 1990) and forest degradation (Laurance *et al.*, 2001; Werth & Avissar, 2002; Nepstad *et al.*, 2004). Regional climate change models nested within global climate models are being developed, but these will require further interpretation to identify the potential impact of climate change at the regional level.

The weather over the Amazon and along the Andes is a good example of how wind patterns and topography are responsible for creating the precipitation patterns that define the natural ecosystems of the region. Understanding the relationships between topography, wind and precipitation is essential to decipher the nature of past climates and ecosystems, to understand and map the current distribution of species and to model how future change will impact upon conservation strategies. In this study, we describe the relationship between topography, wind and precipitation and use climate data derived from multiple sources to validate that descriptive model. We postulate that the distribution of plant species on the eastern slope of the Andes and adjacent regions of the western Amazon is constrained by precipitation gradients that are independent of a latitudinal gradient and test that hypothesis using floristic data based on plant collections.

INFORMATION SOURCES

We use information derived from three public-domain data sets that have been made available over the past several years. Topographic data consisted of digital terrain elevation data (DTED) collected by the NASA Shuttle Radar Topography Mission (SRTM); the continental mosaic was compiled at the Centre for Applied Biodiversity Science at Conservation International using data downloaded from the EROS Data Centre (Fig. 1a). The precipitation data are from the WorldClim grid (Hijmans *et al.*, 2004), which is a 1-km interpolation from 50 years of ground station data (Fig. 1b,c). We compared the WorldClim data set with GOES-8 satellite imagery available from public websites (http://goes.gsfc.nasa.gov/) and which have been collated into summary data sets spanning 2 years (Figs 2 & 3).

The remote sensing data measure the temperature of the Earth's surface; the coldest temperatures are those associated with cloud-tops; the colder the temperature, the higher the altitude of the cloud-top. In the tropics, cold clouds are associated with active deep convection (thunderstorms), thus a high frequency of cold clouds is an indication of heavy rainfall. Data are summarized by showing the frequency of pixels colder than a certain threshold value. Figure 3 shows the frequency of days over the Neotropics where the threshold value temperature was exceeded for a given value [−12°C *c.* 7000 m above sea level (a.s.l.); −38°C *c.* 10,000 m a.s.l.; −65°C *c.* 14,000 m a.s.l.]; high values indicate increased cloud frequency at that altitude. The −12°C threshold registers cold surface temperatures over the altiplano and Andean peaks during winter, so it is not as good an indication of cloudiness as the other two threshold values. The −38°C (235 K) threshold agrees with the widely used GOES precipitation index (GPI); Arkin (1979) showed this value had the highest correlation between tropical rainfall and cloud frequency. The −65°C threshold shows where very high cloud tops are associated with deep convective storms and high rainfall rates.

The high frequency of high/cold clouds in the extra-equatorial super-humid regions (Fig. 2) corresponds to the high rainfall documented by the WorldClim data set. However, the cloud data reveal an artefact in the WorldClim data set, which tends to show the super-humid regions as having an ovoid shape that extends well into the adjacent Amazonian lowlands. The cloud-density data show that these super-humid regions are actually ellipsoidal and are spatially associated with the montane slopes and piedmont of the Andes. In most cases the high-precipitation zones extend laterally on the piedmont and upslope into the mountains further than shown in the WorldClim data set. These discrepancies are caused by the extrapolation of data from too few ground-based sites in the tropical montane and lowland regions of South America (Fig. 1c). This artefact is a potential source of spatial error for models that rely on the WorldClim data set, particularly those that attempt to predict species distributions based on elevation and precipitation.

The WorldClim and satellite data sets are not in good agreement for the high-rainfall region in eastern Ecuador. WorldClim shows this area to have annual precipitation in excess of 5000 mm year^{-1}, but lacks the typical high/cold cloud frequency characteristics of other high-precipitation

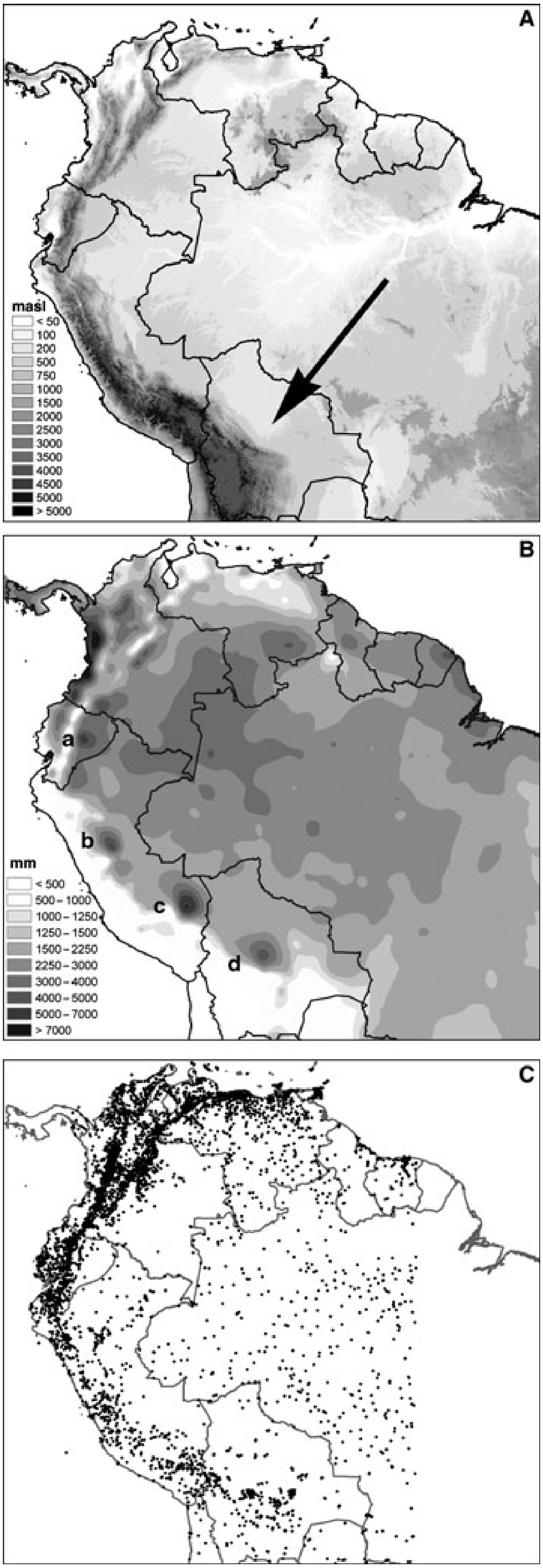

Figure 1 (A) The topography of South America; from the SRTM digital terrain model (NASA/JPL), the arrow indicates the elbow of the Andes. (B) Mean annual precipitation of northern South America, the grey scale shows precipitation from 9000 to <200 mm year^{-1}. The high precipitation zones are: (a) Amazonian Ecuador (maximum precipitation > 5000–5500 mm), (b) Selva Central in Peru (maximum precipitation > 5000–5500 mm), (c) Manu–Tambopta in Peru (maximum precipitation > 7000 mm) and (d) Chapare in Bolivia (maximum precipitation > 5000 mm). (C) The climate station localities upon which the WorldClim data set is based (Hijmans *et al.*, 2004).

regions (Fig. 2). The explanation for the lack of correspondence of the two independent sources of information must be a result of the type of precipitation in Amazonian Ecuador. The absence of a distinct maximum in the frequency of high/cold cloudiness suggests that a significant fraction of the precipitation in eastern Ecuador originates from clouds having a shallower vertical extent.

The wind data come from two sources. The most widely available source is the NCEP/NCAR 'reanalyses' (Kalnay *et al.*, 1996) that have been generated at 6-h intervals using a global prediction model and a data stream from the global meteorological observation data base (http://www.cdc.noaa.gov/index.html). The NCEP/NCAR reanalyses are used for studies of climate variability and are considered to be of acceptable accuracy for studies of larger-scale atmospheric circulation (Fig. 4).

The second source of wind information comes from special observations made during the South American low-level jet experiment (SALLJEX) and associated data collected by the Pan American Climate Studies programme sounding network (PACS-SONET) (http://www.nssl.noaa.gov/projects/pacs/). The SALLJEX observations were made in late 2002 and early 2003, and show finer-scale aspects of air flow over the region. Additional information on the relationship between the South American low level jet and the South American monsoon was obtained from published summaries (Douglas *et al.*, 1999; Nogués-Paegle *et al.*, 2002; Marengo *et al.*, 2004).

The floristic data come from the TROPICOS data base at the Missouri Botanical Garden, the world's largest data base of plant information that contains web-searchable records for over 980,000 plant names and nearly 2.8 million specimens (http://mobot.mobot.org/W3T/Search/vast.html). TROPICOS is the most comprehensive information resource for the flora of the Andean region (Brako & Zarucchi, 1993; Jørgensen & León-Yánez, 1999). TROPICOS was queried using a GIS interface to return all georeferenced specimens that were collected in four super-humid regions (Amazonian Ecuador, Selva Central and Manu–Tambopata in Peru, and Chapare in Bolivia), four intermontane dry valleys (Marañon and Apurimac–Urubamba in Peru; La Paz and Rio Grande in Bolivia) and three intermediate humid regions situated between the super-humid regions (the Condor region in the Amazonas Department in northern Peru, the Purús region in central Peru and the Madidi region in northern Bolivia). Only specimens identified to the species level were used in the analysis and infraspecific taxa were treated as the same species in the floristic analysis; the list was reviewed to exclude cultivated species and orthographic variants, as well as obvious errors in the georeferenced data.

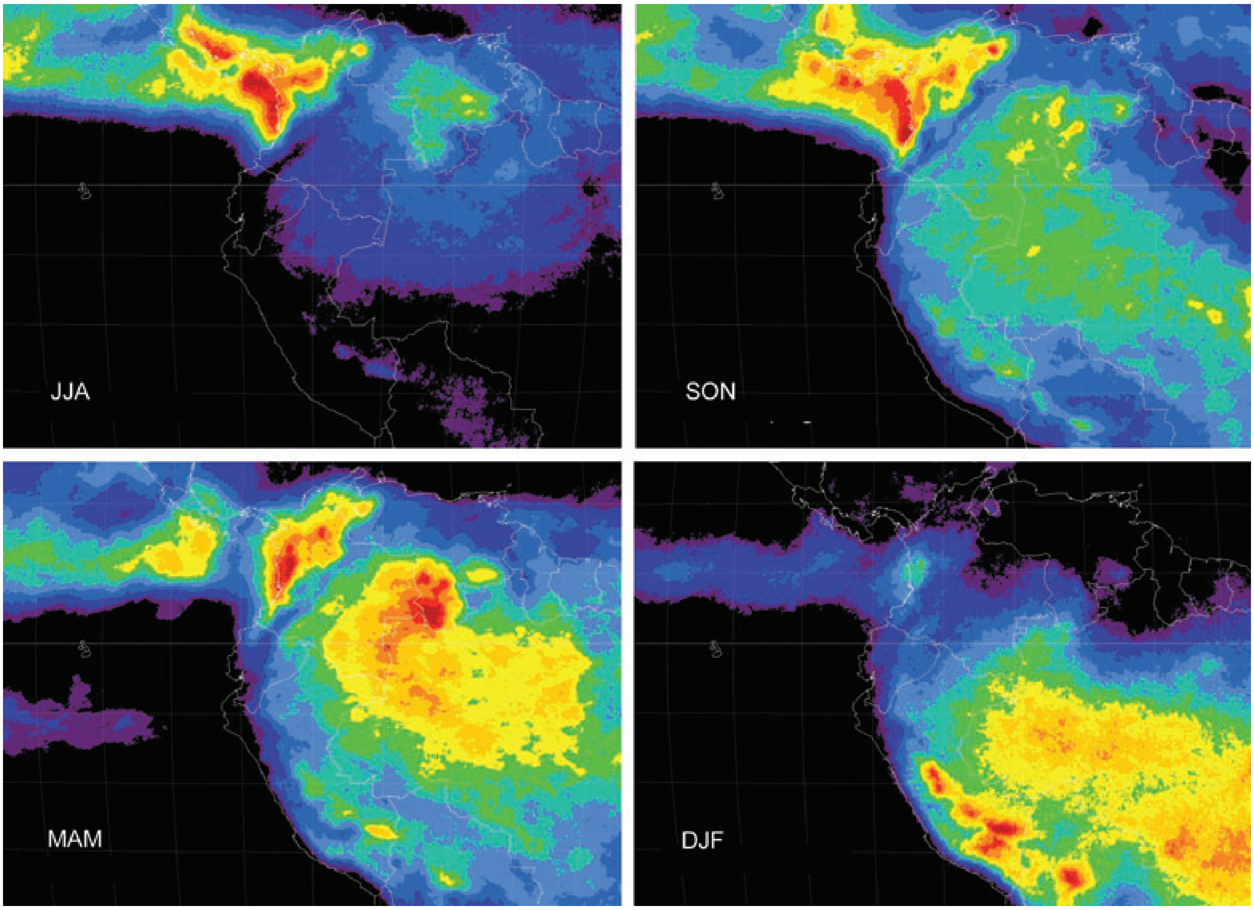

Figure 2 Cold cloud frequency from imagery for years 2002–03 showing the seasonal shift of cloudiness over the Neotropics. Warmer colours (orange to red) correspond to areas with the highest frequency of clouds with temperatures colder than −38°C threshold, black is zero. Seasons are: JJA (June, July, August), SON (September, October, November), MAM (March, April, May) and DJF (December, January, February). Cold cloud tops are associated with rainstorms and a map of cold cloud frequency is a surrogate for rainfall intensity.

The floristic analysis was conducted among regions using three separate statistical procedures. Sørensen's similarity index [$SI = 2c/(a + b)$] makes pair-wise comparison, where c is the number of shared taxa and a and b are the total number of taxa at two separate localities. The similarity among localities was also measured using both a detrended correspondence analysis (DCA) and a canonical correspondence analysis (CCA). The DCA partitions the variation among ordinate axes based entirely on floristic similarity, while the CCA is a direct gradient analysis where the ordinate axes are weighted by taxa whose distribution are correlated with the defined environmental parameters (ter Braak & Smilauer, 1997). In the analysis, we used three environmental parameters: the latitudinal centroid of each geographical region, the mean elevation associated with the specimens from each region and the mean annual precipitation of the geographical region according to the WorldClim data set (Table 1).

TOPOGRAPHY, WIND AND RAIN

Starting in the late 1990s, meteorologists began to document the wind flow patterns at Santa Cruz, Bolivia and described what has long been known to the residents of the region; relatively steady and strong winds blow from the north-west to the south-east (Douglas *et al.*, 1999). These local winds are now known to be a manifestation of a much larger atmospheric phenomenon that impacts upon many of the continent's ecosystems east of the Andes. The winds are associated with a major gyre that originates with the Atlantic trade winds that pass over the Amazon Basin and recurve southward as they near the Andes to form the South American low level jet (SALLJ; Nogués-Paegle *et al.*, 2002; Marengo *et al.*, 2004). This wind system can be viewed as a river of humid air that parallels the Andean Cordillera, which eventually turns south-eastward and flows towards southern Brazil, north-western Argentina and the Atlantic Ocean.

The tropical rain forest ecosystem of the Amazon basin is dependent on the humid trade winds that flow from the Atlantic, transporting water from the ocean to the continent. Rainfall associated with this moisture influx migrates seasonally from the north-west to the south-east across the Amazon Basin (Hastenrath, 1997), and the period with the greatest precipitation and frequency of cold cloudiness in the south occurs during the austral summer (Fig. 2). Water is recycled

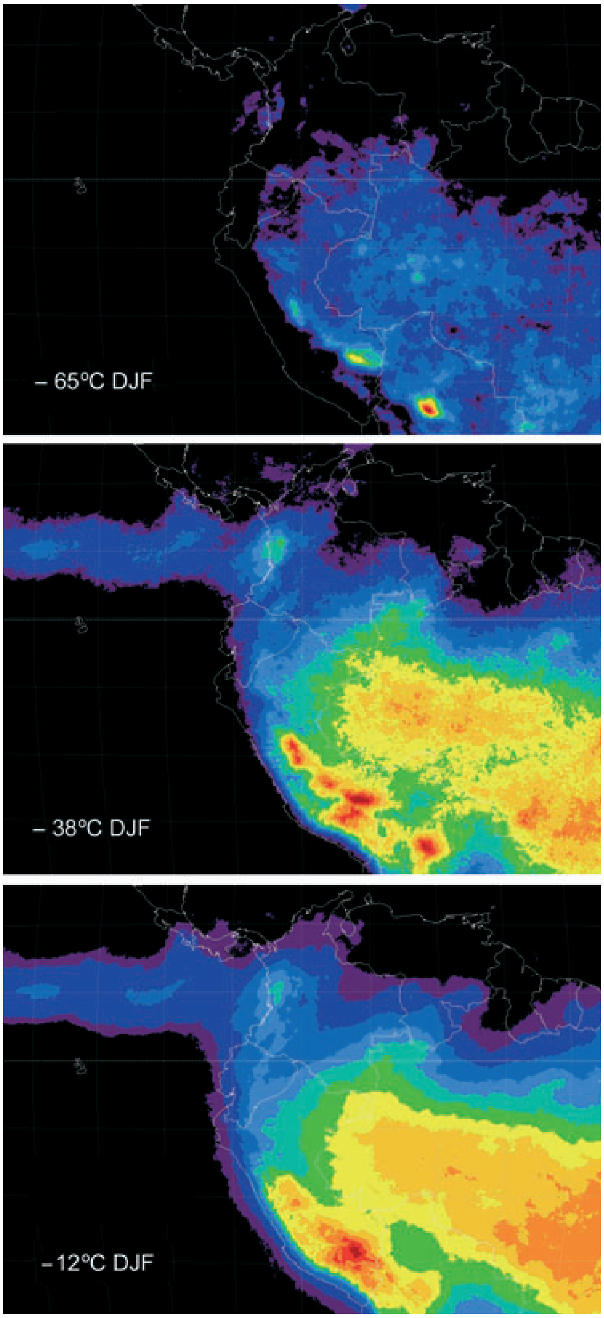

Figure 3 Frequency of clouds for different temperature thresholds over the Neotropics averaged over the austral summer months of 2002 and 2003; the temperature threshold is inversely correlated with the altitude of the cloud tops, and higher clouds are correlated with greater precipitation. The colours orange to red correspond to highest frequency of clouds with temperatures that are colder than the three temperature thresholds. The areas with the highest frequency of coldest clouds correspond to the regions with highest rainfall. Data derived from the GOES-8 satellite.

within the Amazon Basin in the form of precipitation and evapotranspiration and the westward-flowing trade winds remain humid until reaching the Andean Cordillera. Until the documentation of the SALLJ, the general assumption was that winds continued to flow westward and precipitation occurred as part of the orographic uplift of the trade winds against the eastern slopes of the Andean cordillera. The aridity of the high Andes and the Pacific Coast reinforces this view since a rain shadow is a natural consequence of orographic rain (Humboldt, 1807). Some of these winds at relatively high altitudes pass through the Huancabamba Gap on the border between Ecuador and Peru, but others are recurved towards the south to form the SALLJ.

The impact of the SALLJ is most noticeable over eastern Bolivia during the austral summer, when the region of maximum rainfall is displaced southward over South America in association with the beginning of the wet season of the South American summer monsoon (Nogués-Paegle *et al.*, 2002). The SALLJ is responsible for much of the transport of moisture from the Amazon Basin into the seasonally dry regions of subtropical South America (Fig. 4) and is responsible, together with convective processes, for much of the annual precipitation in south central and southern Brazil, as well as in northern Argentina and Paraguay (Nogués-Paegle *et al.*, 2002; Marengo *et al.*, 2004).

The traditional view of many geographers has been of a rain forest situated at the base of the eastern slope of the Andes (Montgomery *et al.*, 2001) supplied with moisture by the Intertropical Convergence Zone (ITCZ). Mean annual precipitation was assumed to decease with increasing latitude due to the seasonal shift of the rain belt associated with the ITCZ and the impact of increasingly pronounced dry seasons (Maslin & Burns, 2000). Even today, routine reports from meteorological services in Peru and Bolivia refer to the movement of the ITCZ over the region, a concept that is not generally accepted by research meteorologists. The compilation of better data sets and the increased awareness of the South American summer monsoon and the SALLJ revealed an important interaction between topography and wind. Figure 1b shows the precipitation patterns as revealed by the WorldClim data set that show considerable variation in rainfall along the eastern slope and piedmont of the Andes. This variation can be partially understood when viewed in the context of the SALLJ and the orientation of the Andes.

The Andes are generally visualized to have a north–south orientation, but the central Andes actually form a curving arc, the Bolivian orocline (Hinsch *et al.*, 2002; McQuarrie, 2002). At 18° S the Andes abruptly change orientation, forming the 'elbow of the Andes' (Fig. 1a). The topographic setting associated with the Bolivian orocline is largely responsible for channelling the SALLJ back to the east, while local variations in topography are associated with the variations in precipitation observed on the piedmont south of the equator (Figs 1b & 2).

Super-humid regions in the Andean foothills and piedmont

The impact of the low-level winds east of the Andes is best understood when viewed in the context of the regional

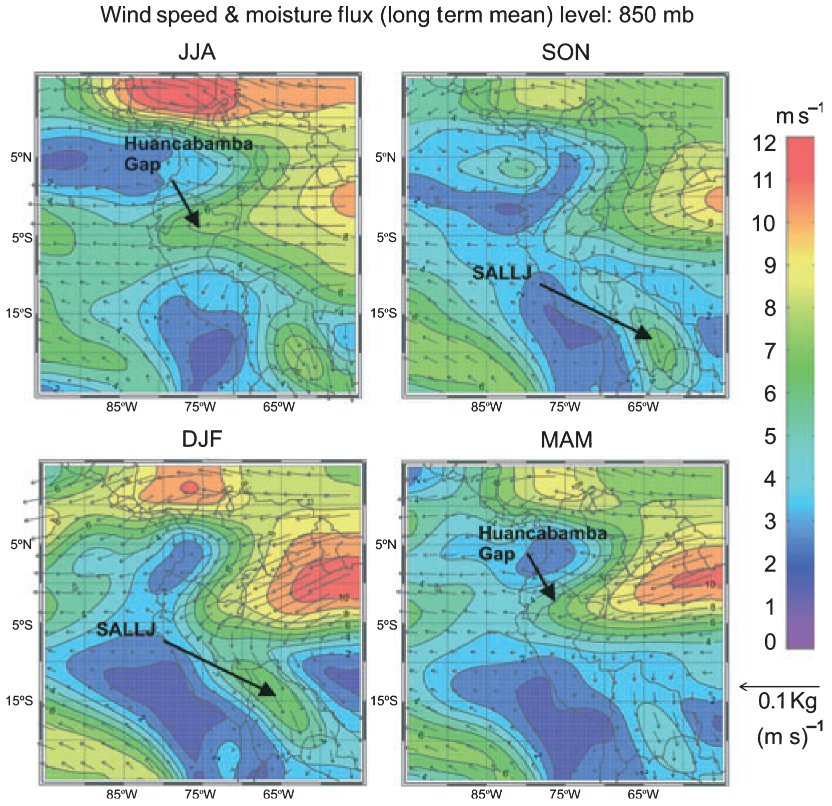

Figure 4 Moisture flux patterns over the western Amazon and central Andes. The length of the moisture flux vectors is proportional to magnitude of the moisture, while the direction of the vectors gives the direction of the prevailing wind. The South American low-level jet (SALLJ) flows from the north-west over eastern Bolivia all year, but is strongest during the austral winter. The seasonal mean wind speeds (contours, in m s^{-1}) show the strong trade winds entering from the Atlantic with significant recurvature to the south throughout the year (vectors). However, wind flow occurs over the Andes at the Huancabamba Gap throughout the year. Data are from the NCEP/NCAR reanalyses and represent the period 1950–2003. The 850 mbar level is approximately 1500 m above sea level and is near the level of maximum winds of the SALLJ.

geological and topographic setting. Due to its equatorial location, the piedmont and foothills in Ecuador receive cross-Amazonian trade wind flow all year round and, consequently, are one of the wettest regions within the Amazon Basin. However, there are three additional well-defined and separate high-rainfall areas situated well to the south of the equator that have values of mean annual precipitation in excess of 3500 mm and up to 6000 mm in places. These sites include the foothills north-east of central Peru (Selva Central), the Manu–Tambopata region in southern Peru and the Chapare region of Bolivia (Fig. 1b). Between each of these four high-precipitation regions there are extensive zones on the piedmont and in the adjacent foothills where mean annual precipitation rarely exceeds 2500 mm.

The SALLJ is a dominant climatic feature along the eastern slopes of the central Andes and over the south-west Amazon Basin (Marengo *et al.*, 2004). The mean wind velocity and the frequency of windy days increase between 12 and 18° S; this wind pattern is associated with the two southern very-high rainfall zones in Manu–Tambopata and Chapare. Both super-humid regions are associated with mountain ranges with a more east–west orientation with regard to mean wind flow, and present relatively abrupt vertical profiles rising between 4000 and 5000 m over a horizontal distance that is only 50–80 km wide. Consequently, winds have a considerable upslope component that results in high annual precipitation. In adjacent regions, where the topographic contours are more nearly parallel to mean wind flow, there is less rainfall (Fig. 4). At 18° S, the orientation of the Andes radically changes, but the SALLJ winds continue to flow to the south-east away from the Andes. The south-eastward flow descends in the lee of the high terrain, the subsiding air suppresses cloud development, and this leads to dramatic decrease in precipitation to the south of Santa Cruz (Figs 1 & 2).

The high rainfall in the regions noted above is not fully explained by the mean wind flows and topographic orientation during the warm season months; cold cloud tops are registered in the early morning in high-precipitation regions (Figs 5 & 6). This observation suggests that much of the rainfall in these wet spots is due to early morning precipitation on the piedmont adjacent to the mountain slopes, whereas the precipitation at higher terrain appears to maximize during the afternoon hours.

The regions of highest rainfall and cloudiness (Chapare, near Manu–Tambopata, central Peru) are all regions where the maximum precipitation occurs in the early morning hours. The diurnal cycle composites (Fig. 5) suggest that nocturnal drainage flows from surrounding higher terrain are associated with the initiation of convective storms, a mechanism that has been described for other tropical regions. Descent along the sloping terrain in the early morning requires compensatory rising motions over the adjacent piedmont; with enough lifting, saturation of the unstable air leads to the development of convective storms that persist until a few hours after sunrise. Thus an additional reason for the enhancement of precipitation in wet spots may be due to favourable configurations of

Table 1 Botanical collections and total number of identified taxa (species and subspecies) from the different climatic regions.

	Latitudinal midpoint	Mean elevation (m)	Mean annual precipitation (mm)	Number of specimens	Number of determined specimens	Total number of identified species
Dry valleys						
Marañon	6.00	1561	945	7855	3064	1632
Apurimac	13.00	1698	1431	1246	745	621
La Paz	16.10	1895	914	1681	1062	845
Rio Grande	18.50	1823	753	1825	1162	764
Humid regions						
Condor Amazonas	4.40	335	2704	5295	1972	1403
Purús	11.20	212	2329	2060	1203	891
Madidi	14.50	401	2009	6360	3632	1569
Super-humid regions						
Amazonian Ecuador	1.08	590	3858	30,437	21,953	4458
Selva Central	8.69	372	4269	36	29	28
Manu–Tambopata	13.00	581	4304	4552	1956	1419
Chapare	16.60	250	3916	815	555	429
Total				62,162	37,333	8320

cold-air drainage. The central Peruvian cloudiness maximum is found over the upper parts of the Rio Pachitea, just south of Pucallpa (8° S), a low broad valley that is surrounded by elevated terrain except to the north. Air with a high relative humidity must be present, so that a small ascent will produce condensation and cloud growth. It should be noted that although the discussion above suggests plausible mechanisms of rainfall production that have been documented in many tropical regions, there are no specific studies of the cited regions. Many of the hypotheses could be directly addressed through the application of mesoscale numerical weather prediction models that can simulate the topographically induced flows and associated development of convective storms.

In summary, the interaction of the low-level winds, the diurnal cycle of solar radiation and the particular geography of the Andes leads to the formation of geographically separate high-rainfall areas in southern Peru and central Bolivia. Seasonality is also an important component when evaluating the impact of precipitation regimes on the Andean piedmont. The southern region of the Amazon Basin, especially the south-western part, has a pronounced seasonality and the zones of very high precipitation within that region are more seasonal when compared with the equatorial Amazon. However, they remain 'humid' throughout the year and the estimated evapotranspiration does not exceed precipitation during any month (Hijmans *et al.*, 2004).

Dry valleys, canyons and plateaus

Botanists have long been aware of the presence of dry forest and other xeric plant communities on the eastern slope of the Andes (Troll, 1968; Hueck & Siebert, 1972). Almost all of these communities exist as isolated patches populated by species with an apparent shared biogeographical history (Prado & Gibbs, 1993; Prado, 2000; Pennington *et al.*, 2004). However, relating these habitats to climate maps extrapolated from terrestrial stations has not been feasible due to the thinness of ground-station data. Satellite-derived data have likewise not shown precipitation patterns at sufficient resolution to enable the identification of xeric habitats, although the interpretation of Landsat images has had limited success in identifying some of these regions based on land cover (Killeen *et al.*, 2006). Fortunately, traditional botanical field studies have been more successful in mapping dry forest habitats within the eastern Andes (Kessler & Helme, 2000; Pennington *et al.*, 2000; Ibisch *et al.*, 2003; Cayola *et al.*, 2005).

Dry habitats typically exist in valleys situated behind large or high mountain barriers that create an orographic rain shadow. Rain shadow has been commonly invoked (often erroneously) to explain the distribution of precipitation in the Andes and the presence of arid ecosystems in western Peru, the Bolivian altiplano and northern Chile. However, rain shadow effects alone do not explain the existence of all dry habitats, particularly the extreme aridity that can be found in juxtaposition with some of the world's most humid forests on the same side of the continental divide. The most extreme xeric vegetation types are found within very deep canyons, and it is not uncommon to find vegetation dominated by arboreal cacti in canyon bottoms that are bordered upslope on both sides of the canyon by cloud forests.

The aridity in the deep canyons along the eastern flank of the Andean cordillera can be explained partly as a consequence of the diurnal cycle of solar heating. During the mid-morning to mid-afternoon hours the canyon or mountain slopes are heated by short-wave solar radiation. The resulting difference in density between the air in contact with the heated slopes and the cooler air over the middle of the valley produces a pressure difference that causes the air to move towards the heated slopes and, by continuity, rise upwards along the slopes (Defant,

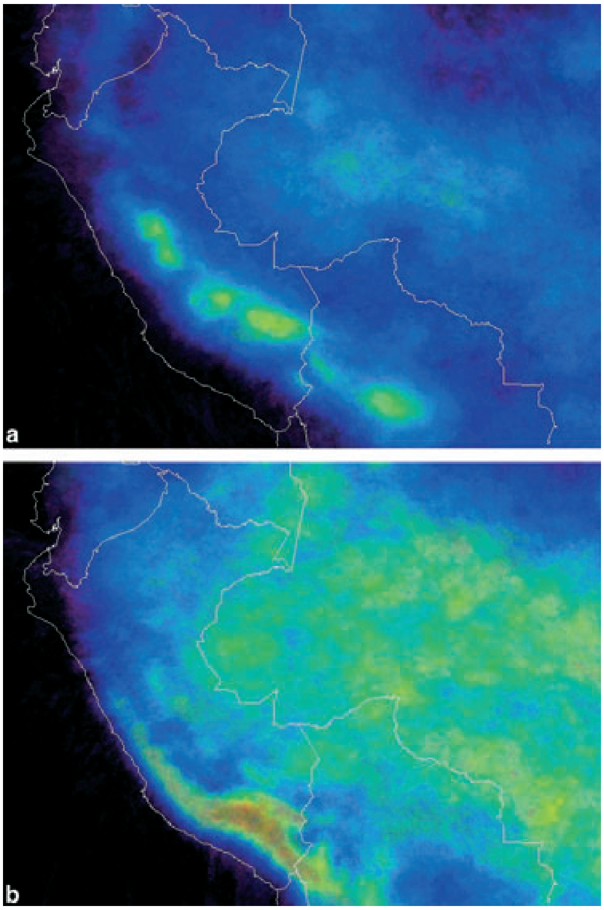

Figure 5 Frequency of clouds colder than −38°C, obtained from averaging hourly imagery from (a) 04:00–13:00 Coordinated Universal Time (UTC) (*c.* midnight to 09:00) and (b) 17:00–02:00 UTC (*c.* 13:00 to 22:00) for two summers (December–March 2002–03). Yellow to reddish (max.) are higher frequencies, blue to black are lowest (black represents zero per cent of time with cold clouds). Note AM maxima are close to the mean precipitation maxima shown in Fig. 1b, indicating that most of the rainfall in these areas occurs in the early morning.

1951; Atkinson, 1981). If enough moisture is initially present in the air and the air rises far enough, it will eventually condense as cloud (Fig. 6). The air rising up the slopes of the canyon must be replaced by air descending over the centre of the valley (Rampanelli *et al.*, 2004). This descending air, although it may start saturated, quickly becomes warmer as it descends and the relative humidity decreases. As a consequence, valley centres are generally cloud-free during the daytime, while the surrounding ridges have a maximum in cloudiness and rainfall during the daytime hours. Comparison of Fig. 6(b) and (c) shows this evolution, which is similar to that discussed by Hindman (1973). The situation is not symmetrical, and there is no corresponding maximum in rainfall over the centre of most valleys late at night. Instead, air descending the mountain slopes forms a relatively cool layer across the canyon floor and continues to descend down the valley. As discussed in the previous section, where the valley floor is broad and flat, and where enough low-level moisture is present near the surface, the lifting induced by the converging winds flowing down both sides of the valley may produce condensation and rain. A similar process appears to be responsible for the nocturnal maxima in rainfall and frequencies of cold cloudiness along the Andean piedmont (Fig. 5a). However, most east Andean dry canyons, especially those linking the altiplano to the piedmont, are relatively narrow and steep, and do not support the development of nocturnal storms. Thus, as these canyons lack both night-time and daytime rainfall they are usually the driest areas along the eastern side of the Andes (Fig. 6).

The minimum of daytime clouds over deep canyons has another effect; more sunlight reaches the surface, increasing the potential evapotranspiration. This higher daily-averaged solar radiation results in higher surface temperatures, lower relative humidities and a more xeric environment in general, compared with other areas with similar annual rainfall, but more daytime cloudiness. This difference in mean daytime cloudiness can be very large between the cloud-free centres of the major Andean valleys that drain eastward and the ridge tops, which are generally cloudy most afternoons.

Implicit in the discussion above is the assumption that the regularity of the diurnal cycle of cloudiness and rainfall over the region is largely responsible for the observed spatial patterns of mean rainfall. Studies like those of Garreaud (2000) and Garreaud & Aceituno (2001) have described intra-seasonal to inter-annual variability of rainfall over the altiplano and have shown that some large-scale conditions (easterly flow for example) are more favourable than others for inducing widespread rainfall. However, the satellite composites shown in Fig. 6(a)–(d), together with the topography (Fig. 1c) suggest that the detailed spatial variability of the mean precipitation field is also strongly influenced by the interaction of topography and the diurnally forced circulations.

It should be noted that most studies of rainfall or cloudiness over the altiplano and surrounding regions (e.g. Garreaud, 2000; Vuille & Keimig, 2004) have used satellite imagery data sets with a pixel size of 30 km or larger from the International Satellite Cloud Climatology Project (ISCCO; Rossow & Schiffer, 1991). The study of diurnal variation of cloudiness over South America by Garreaud & Wallace (1997) modified the original 30 km ISCCP data to a 55 km set; such coarse resolution imagery cannot resolve even the larger canyons that drain the eastern Andean slopes and the role of such canyons in modulating local rainfall cannot be inferred from studies using such data. The higher-resolution imagery used in this study to produce Fig. 6 is needed to depict the cloudiness gradients more accurately.

Recently, accurate and well-validated vegetation maps of the Bolivia Andes have shown the distribution of the dry forest and scrub vegetation in the country (Navarro & Maldonado, 2002; Ibisch *et al.*, 2003). Similar detailed information for Peru has yet to be produced, but a preliminary review of Landsat images and fieldwork shows that xeric vegetation is present in the

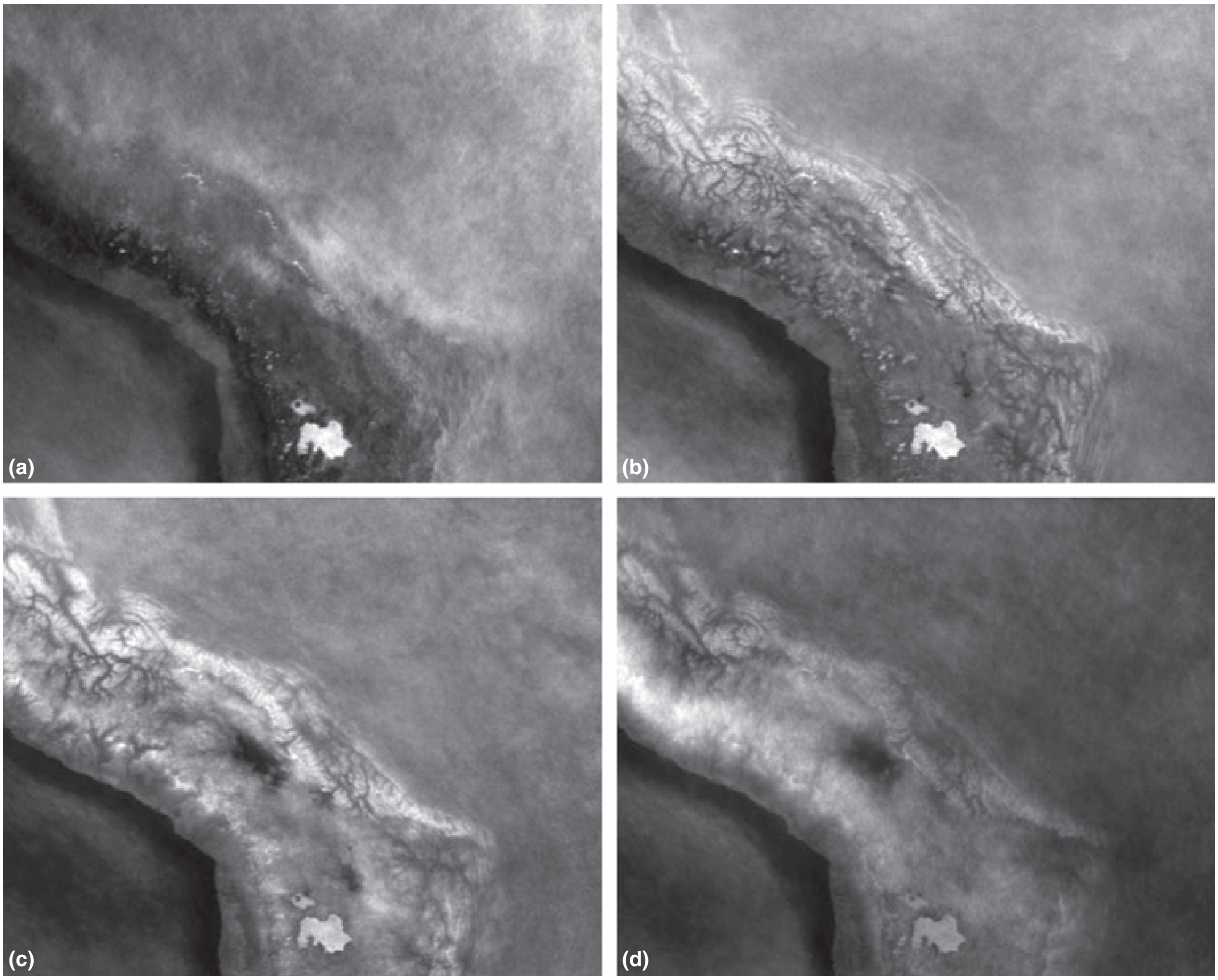

Figure 6 Mean cloudiness from 4 months (December–March 2003–04) of GOES-8 visible light imagery (brighter is more clouds) at four times during the diurnal cycle. (a) 11:45 UTC (07:45 local), (b) 14:45 UTC (10:45 local), (c) 17:45 UTC (13:45 local) and (d) 20:45 UTC (14:45 local). Note that the deep valleys of the central Andes become increasingly cloud free as the day progresses.

canyons of the Apurimac and Marañon rivers (Fig. 7). The two complimentary topographic phenomena of rain shadow (prevailing winds interacting with topography) and deep canyons (topography interacting with the diurnal cycle of solar heating) provide an effective explanation for the presence for almost all of the dry forest habitat patches on the eastern slope of the Andes in Peru and Bolivia. However, there is one locality, near the Peruvian and Bolivian border, which cannot easily be attributed to either rain shadow or deep canyon effects. A small plateau situated adjacent to Madidi National Park is covered by deciduous forest and grassland within a broader region that is otherwise characterized by evergreen forest (Killeen *et al.*, 2006). Originally, ecologists ascribed the formation of these dry habitats to degradation of the ecosystem caused by past human societies, but more recent surveys have shown it to be a naturally occurring ecosystem characterized by several endemic bird species (Herzog & Kessler, 2002) and an adjacent valley is covered by more than 40,000 ha of undisturbed dry forest habitat (Kessler & Helme, 2000). Rain shadow has been invoked as an explanation for the development of the forest and savanna, but an examination of the region using a geographical information system indicates that the ridges situated upwind are not particularly high and do not provide a convincing explanation for the formation of such a large dry forest formation (Killeen *et al.*, 2006).

From a meteorological perspective, it is likely that a satisfactory explanation of this dry forest and savanna region, as well as other important variations in mean precipitation seen along the eastern side of the Andes, will only come from a systematic application of high-resolution atmospheric simulation models that can reproduce the topography of the region at high (~1 km or less) spatial resolution. By simulating the atmospheric evolution under conditions that represent the commonly observed large-scale flow regimes it should be possible to reproduce the observed patterns of rainfall and cloudiness.

Dry habitats have played an important role in the evolution of biodiversity in the Andes. By providing a functionally distinct vegetation type with a unique biota, and acting as an obstacle to the dispersion of species restricted to humid

Figure 7 The 10 subregions included in the floristic analysis; light grey are dry valleys, dark grey are humid regions, black are super-humid regions; the humid and subhumid polygons were derived from the WorldClim data set (Hijmans *et al.*, 2004), while the dry region polygons were derived from the SRTM digital elevation model and identify the dry valleys of the eastern Andes (see Fig. 1).

habitats, dry forests promote potential allopatry. In particular, cloud forests are often surrounded by, or interposed with, dry habitats, thus contributing to the isolation and evolution of the numerous endemic species characteristic of these ecosystems. Dry valleys and canyons situated on the eastern slope of the Andes offer a particularly hospitable environment for human settlement, being climatically benign with respect to the abundant parasites and diseases characteristic of the humid tropics, but enjoying ample water resources for agriculture and domestic use. Dry valleys show extensive evidence of early human habitation, as well as later advanced civilizations in the pre-Hispanic era (Mesa *et al.*, 1998).

ENVIRONMENTAL GRADIENTS

The relative importance of latitudinal and precipitation gradients in influencing species distributions was evaluated by comparing the floristic similarity among nine spatially distinct regions.

The TROPICOS data base reveals that the Andes and adjacent regions of the Amazon have not been subject to an adequate biological survey. The super-humid region in central Peru (Selva Central) is potentially one of the most diverse places on the planet, yet a mere 36 collections have been registered for this region; the super-humid Chapare region in Bolivia is not far behind with only 865 specimens (Table 1). Amazonian Ecuador has the highest collection density, yet this reflects an incomplete inventory. The Manu–Tambopata region has been the subject of intensive research for more than 30 years, but only a moderate number of specimens were registered in TROPICOS.

Table 2 Number of taxa shared among the three different climatic regions studied; values in the lower left half of the matrix are Sørensen's similarity index.

Regions	Dry valleys	Humid regions	Super-humid regions
Dry valleys		1351	856
Humid regions	0.43		1761
Super-humid regions	0.21	0.43	
Total number of taxa	3242	3012	5209

Regardless of the limitations of the data set, the 8449 species registered for the 10 different subregions represent a sample of the flora of the different regions, and the floristic data show several trends. Dry valleys have floras that differ radically from those of both humid and super-humid regions (Tables 2 & 3); this information is already known to botanists and validates the utility of the data set (Pennington *et al.*, 2004). The floristic analysis also reveals some novel features about the dry valleys and their floras. First, dry valley floras show levels of within-group similarity that are only marginally greater than these regions share with adjacent humid regions. Second, northern (Amazonian) dry valleys are more similar to one another than they are to the southern (Chacoan) Rio Grande Valley. The level of similarity measured for the humid and super-humid regions reveals a geographical gradient, and that humid and super-humid regions, although broadly similar, also have regional differences (Table 3).

Sørensen's index offers a simple numerical value that measures floristic similarity, but it is a one-dimensional measurement based on a simple comparison between two samples. Ordination procedures permit a multi-dimensional and multi-sample comparison and can be used to identify and characterize gradients among samples. The ordination procedures were applied to a pooled data set that included all of the species for all 10 subregions (Fig. 8), as well as a series of separate analyses performed for each of 37 plant families and pteridophytes that are considered to be either diverse or characteristic of tropical forest ecosystems, include a variety of life forms, and which have benefited from the study of specialist taxonomists over the past two decades (see Figs S1–S5 in *Supplementary Materials*). The DCA analysis of the pooled data set shows that dry valleys are not only different from humid and super-humid regions, but are also relatively dissimilar among themselves (Fig. 8). The differentiation of dry valleys was accentuated when the data were analysed by the CCA, in part because these areas also had mean elevations greater than both the super-humid and humid regions. Of all the dry valleys, the most similar to humid regions was the Marañon Valley (Table 3), which also had the greatest number of collections (Table 1), highlighting the limitations of the data set and the possibility that at least some of the differences or

Table 3 Taxa shared by the different regions. Boxes surround sample comparisons with similar precipitation regimes (dry, humid, super-humid); the lower-left half of the table shows the Sørensen's similarity index; values >0.20 are in bold face.

	Marañon	Apurimac	La Paz	Rio Grande	Condor/ Amazonas	Purus	Madidi	Amazonian Ecuador	Manu	Chapare
Marañon		161	190	101	230	130	254	521	214	52
Apurimac	0.14		101	33	92	97	155	205	110	35
La Paz	0.15	0.14		145	76	56	155	184	105	38
Rio Grande	0.08	0.05	0.18		15	16	73	62	16	15
Condor Amazonas	0.15	0.09	0.07	0.01		281	356	934	397	128
Selva Central	0.10	0.13	0.06	0.02	**0.24**		376	518	310	140
Madidi–Tambopata	0.16	0.14	0.13	0.06	**0.24**	**0.31**		757	416	259
Amazonian Ecuador	0.17	0.08	0.07	0.02	**0.32**	0.19	**0.25**		806	256
Manu	0.14	0.11	0.09	0.01	**0.28**	**0.27**	**0.28**	**0.27**		169
Chapare	0.05	0.07	0.06	0.03	0.14	**0.21**	**0.26**	0.10	0.18	
Total	1632	621	845	764	1403	891	1569	4458	1419	429

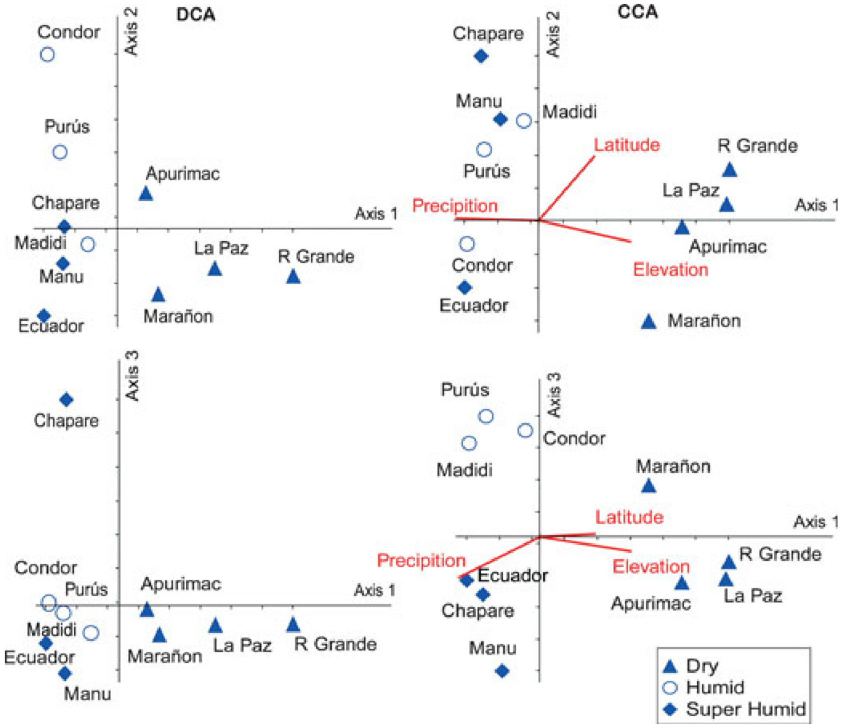

Figure 8 Depiction of the floristic similarities using detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA); the analyses were based on the presence or absence of 8318 species in 10 geographical regions defined by precipitation regimes (see Fig. 7 & Table 1); symbols are geographical regions and radiating lines in the CCA plot depict the direction and strength of environmental variables. Monte Carlo test results for the CCA eigenvalues were $P = 0.03$ (axis 1), 0.03 (axis 2) and 0.07 (axis 3) and for species–environment correlations were $P = 0.04$ (axis 1), 0.04 (axis 2) and 0.08.

similarities observed among regions are the result of collecting artefacts.

Humid and super-humid areas were not discriminated as being floristically distinct by the DCA and these six regions were consistently grouped together with varying degrees of similarity, thus demonstrating the broad similarity of the humid forest flora along the Andean piedmont and the eastern flank of the Andes. However, the CCA did discriminate among the humid and super-humid regions for pooled data (Fig. 8), as well as for 29 of 39 families when analysed individually (see in Supplementary Figs S1–S5). For the pooled data, precipitation was negatively correlated with the first ordinate, while the second ordinate corresponds to a latitudinal gradient that is evident among the humid and subhumid areas jointly, as well as for the dry valleys separately (Fig. 8). In addition, there is a separate trend associated with the third CCA axis that demonstrates that super-humid regions are different in their floristic composition when compared with adjacent humid regions and that this difference is at least partially explained by precipitation.

In summary, the CCA showed that there are measurable differences in the floristic composition of dry, humid and super-humid regions and that these differences can be attributed to latitude and precipitation, as well as elevation. Dry valleys were discriminated using both the DCA and CCA; humid and super-humid regions showed greater floristic similarity, but were discriminated by the CCA when latitude and precipitation were incorporated into the analysis. We identified two separate – but related – biodiversity gradients, one is correlated with geographical proximity, as measured by latitude, and the other is correlated with precipitation, which is only partially related to latitude. Floristically intermediate regions reflected their geographical position and precipitation.

PAST AND FUTURE SCENARIOS

Knowledge that precipitation in the western Amazon Basin and over the Andean foothills is modulated by the interaction of prevailing winds and topography should be used to provide a spatial component for models that attempt to explain the consequences of different climate regimes. The SALLJ is tightly linked to the easterly trade winds and the seasonal evolution of the rainfall over South America; both are a natural consequence of the rotation of the planet and solar radiation, neither of which will disappear under any climate scenario. Likewise, since the orientation of the Andes has been constant over the past several million years, the areas of super-high rainfall and dry valleys are also regions with a high probability of experiencing climate stability, at least when compared with adjacent regions.

Understanding regional patterns of precipitation is important for understanding how past climate regimes have impacted upon the evolution and distribution of biodiversity in the eastern Andes and western Amazon (Bush & Silman, 2004; Mayle *et al.*, 2004). Species diversity decreases with latitude, and one of the assumptions underlying that hypothesis is that high precipitation and reduced seasonality at the equator are important drivers of increased biodiversity (Gentry, 1988; Currie, 1991; Gaston, 2000). If so, extra-equatorial regions of high precipitation in the tropics should likewise have higher levels of biodiversity when compared with adjacent areas with lower levels of precipitation. Unfortunately, the currently available data set is not sufficiently robust to test that hypothesis and underlies the need for both additional biological inventory as well as the integration of data bases, so as to make better use of existing information. Nonetheless, our study does show that the distribution of biodiversity as measured by similarity can also be explained by a precipitation gradient that is independent of latitude.

The once popular refugia hypothesis posited that the humid forests of the Amazon Basin became fragmented during the Pleistocene and that this fragmentation was responsible for the diversification of the Amazonian biota (Haffer & Prance, 2001). The mechanism for explaining the nature of that fragmentation and the subsequent diversification of the Amazonian flora was the presence of a drier and cooler climate, which led to the expansion of savanna ecosystems and a reduction and fragmentation of forest ecosystems. There is little palaeoecological evidence to support the refugia hypothesis (Colinvaux & de Oliveira, 2001) and the prevailing view is that although the spatial extent of humid forest ecosystems was much reduced during the Pleistocene, the Amazon was not fragmented by savanna; more probably, mosaics of evergreen to semi-deciduous tropical forest, according to local hydrology and soils, occupied much of eastern Amazonia, with western Amazonia retaining an evergreen forest (Bush *et al.*, 2002, 2004; Mayle *et al.*, 2004). Similarly, there are explanations other than allopatric speciation that can account for the extremely high levels of biodiversity in the Amazon (Knapp & Mallet, 2003). Chief among these alternative viewpoints are the very great age of the Amazon flora (Wilf *et al.*, 2003) and the existence of marine incursions in the Tertiary that fragmented the South American continent (Rasanen *et al.*, 1995; Webb, 1995; Nores, 1999).

Nonetheless, the lack of evidence to support the refugia hypothesis as the mechanism for the evolution of Amazonian diversity does not rule out the existence of spatial climate variation in the Amazon during the Pleistocene. Quite to the contrary, there is overwhelming evidence of past climate change and of alterations in the distribution of biodiversity (Mayle *et al.*, 2004). The identification of climatically stable zones of high and low precipitation provides the basis to refine further the hypotheses regarding past climates and the distribution of biodiversity in the Amazon and Andes. Regions that are likely to harbour greater diversity (super-humid areas) or increased endemism (isolated dry valleys) should be made a priority for biological inventory. Even more importantly, the knowledge that some areas appear to be inherently climatically stable should be a central theme in conservation planning, particularly in a strategically important region such as the western Amazon and the eastern Andes. Climatic stability is an extremely important asset and the identification of such regions should be incorporated into the very core of conservation planning.

ACKNOWLEDGEMENTS

Images were provided by the NOAA-CIRES Climate Diagnostics Centre, Boulder, Colorado, from their website at http://www.cdc.noaa.gov/. Support for this research was provided by the Critical Ecosystem Partnership Fund (CEPF) to the Noel Kempff Mercado Natural History Museum, and the Moore Family Foundation (to T.J.K.), by the National Science Foundation (grant no. 0101775) and the Taylor Fund for Ecological Research (to P.M.J.). The NOAA's Office of Global Programs supported the research activities of M.D. and J.M.

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SUPPLEMENTARY MATERIALS

The following supplementary material is available for this article:

Figure S1. Results of the canonical correspondence analyses (CCA) for eight selected plant families (Acanthaceae to Bromeliaceae).

Figures S2. Results of the canonical correspondence analyses (CCA) for eight selected plant families (Capparidaceae to Heliconiaceae).

Figures S3. Results of the canonical correspondence analyses (CCA) for eight selected plant families (Lauraceae to Myristaceae).

Figures S4. Results of the canonical correspondence analyses (CCA) for eight selected plant families (Myrsinaceae to Pteridophytes).

Figures S5. Results of the canonical correspondence analyses (CCA) for five selected plant families (Rubiaceae to Zingiberaceae).

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2006.01682.x

BIOSKETCHES

Timothy J. Killeen is a conservation biologist who has resided in Bolivia since the early 1980s. His research interests have evolved over the course of his career, starting with the taxonomy and ecology of grasses, later focusing on floristics, plant community ecology and biodiversity patterns at local and regional scales; efforts to map biodiversity led to an interest in remote sensing and geographical information systems.

Mike Douglas is a research meteorologist with a background in tropical and mesoscale meteorology. His principal focus during the past 15 years has been on Latin American meteorology and climate, with an emphasis on observational studies. Current work is focused towards explaining the characteristics of the observed climate of the region at small spatial scales through application of meso-meteorological concepts.

Trisha Consiglio is a geographical information systems analyst and biodiversity scientist with the Missouri Botanical Garden. She uses a broad array of tools including GIS, remote sensing and species distribution modelling to identify areas of plant biodiversity and endemism. Her current work is focused on integrating these tools with plant systematics to explain patterns of plant distributions and test ideas of niche conservatism on a regional scale.

Peter Møller Jørgensen, Danish botanist, received his PhD from the University of Aarhus in Denmark, and is currently an Associate Curator at the Missouri Botanical Garden. He has coordinated and co-edited the *Catalogue of the Vascular Plants of Ecuador*. During the past 22 years his research has focused on the flora of the tropical Andes and he is the author of many papers and several books on this topic.

John Mejia hails from Medellin, Colombia, where he received an education in hydrology and worked on projects related to water balance and climate forecasting. He is currerntly a PhD candidate in the meteorology department at the University of Oklahoma. His dissertation research into aspects of the American monsoon system has involved extensive field work, analysis of satellite imagery and other meteorological observations, and mesoscale modelling.

Editor: Mark Bush

The inspiration for this special issue on Amazonian biogeography was a meeting of the Association of Tropical Biology held in Uberlândia, Brazil, 24–28 July 2005. The papers comprise several commissioned as an outcome of this meeting, alongside other unsolicited submissions to the journal.