LAND-COVER CHANGES DURING THE PAST 50 YEARS IN THE SEMI-ARID TROPICAL FOREST REGION OF NORTHERN PERU

TONE MARIE EKTVEDT, OLE REIDAR VETAAS and ANDERS LUNDBERG

With 8 figures, 4 tables and 1 appendix Received 22. March 2011 · Accepted 21. February 2012

Summary: Dry forests are under much higher pressure from deforestation than humid forests, yet less attention has been paid to these forests. To develop better management strategies, it is necessary to analyse the dynamics of these forests at different scales and to assess their potential to recover from natural or human disturbances. This study combines broad and fine scales to investigate temporal changes: at broad scale we use aerial photos (from 1949, 1962, and 1999) and GIS to document land-cover change during a long-term period of 50 years; at fine scale we use spatial gradient analyses to document changes in species composition during a short-term period of four years. Re-sampling of the same elevational gradient (100-460 m a.s.l.) provides both a spatial and temporal gradient. Plausible causal links between human impact and documented changes are evaluated by means of ordination and Monte Carlo permutation tests. Density and diversity of seedlings, juveniles, shrubs, and trees were investigated in permanent plots from 2003 to 2007 along an elevational gradient. Approximately 17% of the forest has been lost during the last 50 years; giving an annual forest decline of 0.33%. The forest degradation during the 50 years in northern Peru was mainly due to agricultural expansion. During 1949–1962 forest declined by only 1.7%, while a greater forest decline took place during 1962–1999 (15% decline). Reasons for the greater forest loss during 1962-1999 are discussed. A new agrarian land reform from 1969 and population increases are likely reasons. The gradient analyses show a clear increase in species richness and spatial turnover in species composition along the elevational gradient. The ordination analysis reveals a significant change in species composition from 2001 to 2005, and we hypothesise that this may relate to browsing and logging activities. Although the number of faeces and signs of logging did not have a significant correlation with the ordination axes, the Monte Carlo permutation test in redundancy analysis (RDA) reveals a significant effect of browsing on species composition. The changes in species richness and species composition with elevation may be due to climatic differences between the lowland and upland mountain study area, rather than different intensity of human land use. Browsing and logging activities take place quite evenly over the entire study area, rather than being restricted to a certain area. Re-sampling of the permanent plots reveals that the lowland species Prosopis pallida was the only species able to survive from seedling stage to juvenile stage during the four-year investigation period. About 30% of the Prosopis pallida seedlings developed into juveniles, which indicates that this species may be better adapted to drought than other species in this environment.

Zusammenfassung: Obwohl tropische Trockenwälder in stärkerem Ausmaß von dem globalen Trend der Entwaldung betroffen sind als tropische Feuchtwälder, wurde ihnen bisher vergleichsweise wenig Aufmerksamkeit zuteil. Um bessere Managementstrategien zu entwickeln, ist es notwendig, die Dynamik dieser Wälder und ihr Regenerationspotential auf unterschiedlichen Skalen zu untersuchen. In der vorliegenden Studie werden großräumige und kleinräumige Untersuchungsansätze kombiniert um zeitliche Veränderungen am Beispiel eines Untersuchungsgebiets im Norden von Peru aufzuzeigen. Die großräumige Analyse stützt sich auf Luftbilder aus den Jahren 1949, 1962 und 1999; der kleinräumige Ansatz beleuchtet im Zuge einer räumlichen Gradientenanalyse, die Veränderungen der Artenzusammensetzung innerhalb eines Betrachtungszeitraums von vier Jahren. Als Folge des Landnutzungswandels bzw. der Ausweitung und Intensivierung der agrarischen Nutzung, ist eine Abnahme der Waldfläche von ca. 17% zu verzeichnen. Eine Gradientenanalyse zeigt die deutliche Zunahme der Artenvielfalt und des Artenwechsels entlang des betrachteten Höhengradienten (100 - 460 m NN). Statistische Analysen zeigen zudem, dass sich die Artenzusammensetzung zwischen 2001 und 2005 signifikant verändert hat. Die Zusammenhänge mit veränderter Beweidungs- und Holznutzung, aber auch klimatischen Einflüssen werden diskutiert. Exemplarisch wird anhand einiger Arten aufgezeigt, dass unter den gegebenen Umweltbedingungen und -veränderungen nur wenige Individuen einzelner Arten (z.B. Prosopis pallida) das Keimlingsstadium überleben und somit die Bestandsverjüngung gewährleisten können; innerhalb des vierjährigen Betrachtungszeitraums aber von anderen Arten nicht eine einzige Jungpflanze das Jugendstadium überlebt hat. Insgesamt verdeutlicht die Studie die extremen Umweltbedingungen, das fragile Gleichgewicht in diesen Lebensräumen und die besondere Tragweite sich ändernder anthropogener Einflüsse.

Keywords: Forest dynamics, deforestation, fragmentation, human impact, matrix, recruitment, fine and broad scales, Prosopis pallida

1 Introduction

Nearly half of the tropical and subtropical forests worldwide are dry forests (MURPHY and LUGO 1986). Dry forests and savannas occupy a fifth of the Earth's land surface and support a large proportion of the world's human population and most of its rangeland, livestock, and wild herbivore biomass (SCHOLES and ARCHER 1997). While there has been a strong global focus on the threats to evergreen rain forests due to their overwhelming biodiversity, tropical dry forests and savannas are also diminishing (JANZEN 1988; MILES et al. 2006), and this may be an even bigger problem since millions of people are dependent on these ecosystems for their livelihood (BEHNKE et al. 1993; SANKRAN et al. 2005; FURLEY et al. 2006). Consequently, dry forests are under higher pressure from deforestation than humid forests and their size has been considerably reduced (FAO 2001). Although tropical dry forest is now considered to be the most endangered ecosystem in the lowland tropics (JANZEN 1988; GILLESPIE et al. 2000; LINARES-PALOMINO and PONCE ALVAREZ 2005), very few studies have analysed deforestation and forest fragmentation in these ecosystems (GILLESPIE et al. 2000; PENNINGTON et al. 2006). Peru has the second largest area of tropical forest in Latin America (FAO 2005). There are 3230 million hectares of dry forest in northern Peru (Tumbes, Piura, and Lambayeque), with 67% in Piura (CABREJOS VÁSQUEZ et al. 2006). The dry forests of Piura Province have a high density and richness of tree species (LINARES-PALOMINO and PONCE ALVAREZ 2005), but it is also claimed that this area is being rapidly destroyed by deforestation and fragmentation (e.g. COTLER and MAASS 1999).

Studies that aim to analyse land-cover changes and to understand the dynamics of dry forests are often conducted over a few years, i.e. less than three years (HAMANN 1985; SOTO 1985; DILLON and Rundel 1990; Armesto et al. 1993; Ferreyra 1993; GUTIÉRREZ et al. 1993; 2000). More recently, long-term investigations have been carried out by applying one scale and one method (e.g. CONDIT et al. 1996; BLOCK and RICHTER 2000; HAMANN 2001; RICHTER 2005; RICHTER and ISE 2005). However, if one aims to understand the dynamics of dry tropical forests, multi-scale analyses are needed (NILSSON and GRELSSON 1995). This is because the spatial and temporal variations in precipitation are very high when the annual precipitation is low (NOY-MEIR 1973), and water is the dominant controlling factor for biological processes in general and dry ecosystems in particular (O'BRIEN 2006; VETAAS 2006).

This is further complicated by the climatic El Niño Southern Oscillation (ENSO) phenomenon that causes severe amounts of precipitation at uneven intervals in north-western South America (BENDIX et al. 2011). Therefore comparable long-term studies at different scales are essential to test fundamental questions about ecosystem stability in climate extremes (HOLMGREN et al. 2006a, 2006b; ZEMMRICH 2007). Ecosystems that appear unstable at fine spatial scales may be stable when viewed at broader spatial scales (VETAAS 1993; ZEMMRICH 2007). Also, relationships which are obvious at broad scales, for example between climate and vegetation, may disappear at finer scales, overridden by the effects of competition and other biological factors (WIENS 1989). Studies conducted on several scales will give a better resolution of domains, of patterns and their determinants, and of the interrelationships between scales (WIENS 1989; FARINA 2006). This type of multi-scale approach is necessary to understand the dynamics of these forests, including how dry forests respond to irregular precipitation patterns (WELTZIN and TISSUE 2003; SCHULZ et al. 2011), and the potential to recover from natural or human disturbances or stress (WIEGAND and JELTSCH 2000; WELTZIN and TISSUE 2003; CHESSON et al. 2004; SCHWINNING et al. 2004). This is also a prerequisite if one wishes to develop better management strategies for dry forests in Peru that are, at present, very little studied (LINARES-PALOMINO and PONCE ALVAREZ 2005).

This study investigates changes in semi-arid forests using three approaches at two levels of investigation: at a broad scale we investigate landcover changes using aerial photos and GIS, and at fine scales we investigate (a) species composition along an elevational gradient from a small forested mountain that was sampled twice (2001 and 2005), and (b) change in individual perennials and regeneration of seedlings by monitoring permanent plots on the same small forested mountain from 2003 to 2007. The broad-scale study covers a period of 50 years, while the fine-scale studies cover a fouryear period. Since human use of dry forests may also contribute to disturbance in these areas, the influence of humans is included and discussed. We developed four objectives for this study:

1. To document land-cover changes at a broad scale during a period of 50 years, based on the interpretation of aerial photos.

2. To test if there are fine-scale changes in woody species composition in a four-year period based on repeated spatial gradient analyses (2001 and 2005).

3. To monitor regeneration of important shrubs and

trees on a fine-scale using permanent plots (2003 to 2007).

4. To discuss plausible causal links between human impact and land-cover changes found at a broad scale and species composition and regeneration on finer scales.

2 Study area

Field work was carried out in Piura Province in northern Peru (05°08'S, 80°09'W, Fig. 1). The study area consists of a flat lowland area with forest and agriculture intermixed, and a small forested moun-

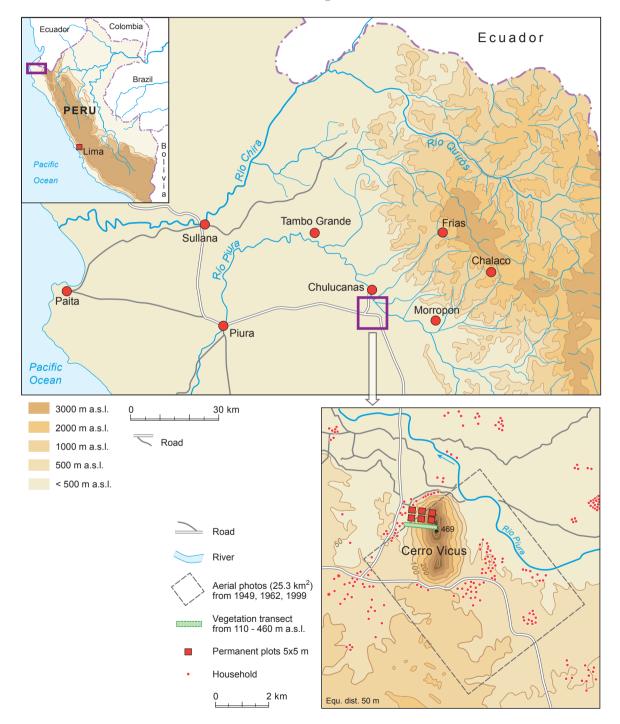


Fig. 1: Map of the study site

tain ranging from 110 to 469 m a.s.l. (Fig. 1). Soil horizons are characterised as AC with soil types of Arenosols and Regosols, and the texture is sandy to clay with medium-sized particles of gravel (INRENA 1998).

Average annual precipitation, excluding ENSO years, is 266 mm¹ in Chulucanas and the area is classified as semi-arid forest (NOY-MEIR 1973; SHMIDA 1985). The precipitation period in northern Peru is usually from November/December to April/May, with a dry period from April/May to November/ December. During ENSO years the increase in precipitation may be severe: precipitation during the ENSO years of 1983 and 1998 was 15.5 and 13 times higher, respectively, than annual average precipitation in the semi-arid environment. During the ENSO event of 1982/83, rainfall in Chulucanas often approached or exceeded 100 mm per day (GOLDBERG et al. 1987). Also, years with no precipitation occur in northern Peru, which is a common feature in dry environments (NOY-MEIR 1973; VETAAS 1993). Temperatures in lowland Piura are stable throughout the year, and the average temperature ranges between 29.5 °C (July) and 33.4 °C (February).

The landscape of the study region is a mixture of different types of dry ecosystems and cultivated fields (INRENA 1998). The dominant forest type is dry open forest and shrub-land in a tropical environment (INRENA 1998). Drought-adapted species like Prosopis pallida (algarrobo) dominate. Other tree species such as Capparis angulata (sapote), Bursera graveolens (palo santo), Loxopterigium huasango (hualtaco), Caesalpinea paipai (charán) and Capparis ovalifolia (vichayo) are also present (CABREJOS VÁSQUEZ et al. 2006; EKTVEDT 2011). Trees in the study area are scattered and adapted to a dry climate, as is typical for semiarid forests in general (NOY-MEIR 1973; INRENA 1998). The semi-arid land is used for agriculture as well as for grazing and browsing activities. The area is impacted by humans, as households are positioned in and close to the study site, with some land areas used for cultivation, while others are used as browsing areas. The forested mountain site is used for browsing, selective logging, and fuel wood collection (EKTVEDT 2011). Regulations on the use of natural resources exist in the study area: It is illegal to harvest trunks of living trees without a written authorisation from Forest Engineers at Instituto Nacional de Recursos Naturales (INRENA) (CONGRESO DE LA REPÚBLICA DEL PERÚ 2000, article 1 (document lack page numbers)). Branches from living trees and dead trees can be collected. Forest resources can be harvested for household consumption, but not for sale. Forest Engineers and the Forest Police (Policía Forestal) control the harvest.

3 Methods

3.1 Aerial photo interpretation

Aerial photos and GIS were used for the broadscale analysis. Aerial photos from 1949 (1:20,000), 1962 (1:60,000), and 1999 (1:30,000) covering an area of 25.3 km² were rectified and land cover as well as land-use units were identified based on field studies and aerial photo-interpretation. The scales and resolution of the aerial photos allowed us to identify individual trees, making it feasible to distinguish between forested and non-forested areas. The semi-arid forests in our study area are classified as 'open forest' by INRENA (1998). 'Open forest' is defined by FAO (2006) as having a canopy cover of between 10% and 30% on a minimum land area of 0.05-1.0 hectares. We defined forest as a minimum land area of 1.0 hectare with tree crown cover of more than 20%. To distinguish the small mountain area from the lowland area, contour lines were drawn on the aerial photos from 100 m a.s.l. to 400 m a.s.l. Cultivated land was seen on the aerial photos as clearly defined borders with land areas used for cultivation of crops (maize, rice, yucca, etc.). Plantation refers to fields with planted trees (lemon, mango, etc.). They were recognised on aerial photos as patches with trees in rows. River denotes areas where moving water was present. Flood plain refers to areas with scarce vegetation cover due to erosion. Roads represent routes for travel or transportation. The roads had sandy soils, with the exception of one main road which had permanent pavement (not in 1949) and was used for motorised traffic. The sandy roads were usually path sized and suitable only for walking. Some, at ca. 2 metres wide, were wide enough for donkeys pulling carts. No distinction has been made between narrow and wide roads in the aerial photo classification. Land areas have been identified as 'fragmented' if a 'road' is visible on the aerial photos and if it divides a formerly continuous patch. Void refers to areas which appear

¹⁾ Monthly precipitation and temperature data from Chulucanas (05°06′12′′, 80°09′57′′), 1942–2006; Proyecto Especial Chira-Piura (PECHP); http://www.chirapiura.gob. pe/principal.php and Servicio Nacional de Meteorológica e Hidrológica del Perú (SENHAMI); http://www.senamhi.gob. pe. Contact persons: Ing. Hector Yauri Quispe, superior of SENAMHI, Piura, Peru, and Ing. Grover Otero, former superior of PECHP, Piura, Peru.

as shadows, and such areas are only found on the 1949 photo.

3.2 Ordination analysis of elevational transect

Vegetation analyses were carried out in 2001 along an elevational gradient on a small forested mountain (Fig. 1), and in 2005 we conducted surveys in the same locations following the same sampling protocol. The surveys were carried out from 29 September to 11 October 2001, and from 3 to 10 July, 2005. We sampled 53 quadrats (5 \times 5 metres) along the elevation gradient from 110 m a.s.l. to 460 m a.s.l. The size of quadrats is within the grain size²⁾ suggested for capturing forests using multivariate techniques based on the concept of minimal area and species-area curves (HALVORSEN ØKLAND 2002; KENT and COKER 1992). We used stratified random sampling along a fixed transect (Fig. 2). The transect consists of 11 rectangles of 30 by 100 metres, where each of the 11 rectangles were divided into 12 smaller sub-rectangles. Five of the twelve sub-rectangles were randomly selected and a 25 square metre quadrat was located in the middle of the sub-rectangle (Fig. 2). We used measuring tapes and a compass to map the quadrats. Each of the eleven rectangles was marked to ensure accurate re-sampling. We identified all species and estimated species abundance for all woody species in each quadrat following the extended version of Hult-Sernader's abundance scale (TRASS and MALMER 1973; Tab. 1).

If species identification was not possible in the field, species samples were brought to botanists at two universities in Piura city (Universidad Nacional de Piura and Universidad de Piura) or the Museo de Historia Natural in Lima, Peru. Due to annual fluctuations in herbaceous plants and seasonality, only perennial plants that were registered in both 2001 and 2005 were included in the ordination to investigate change through time (Appendix 1). During the survey we noticed that a few trees and shrubs that were registered in the 2005 analysis, were absent in the 2001 analysis. Due to the species' size and the short period between the surveys, we interpreted this to be a small degree of inaccuracy in our surveying, and those results were therefore removed from the ordination analysis. Ross et al. (2010) demonstrate that even though the original plot cannot be exactly

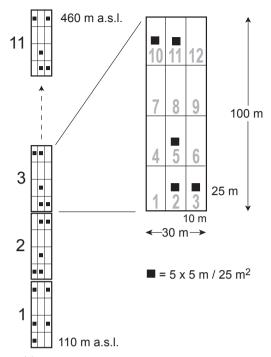


Fig. 2: The 53 quadrats of 25 m^2 ($5 \times 5 \text{ m}$) each were randomly distributed across 11 large rectangles of 30×100 metres covering the bottom (110 m a.s.l.) to the top (460 m a.s.l.) of the mountain

relocated within the vegetation stand, it is possible to detect reliable changes in species composition.

In each quadrat we measured elevation with an altimeter. Settlements are found in the lowland study area, and we assumed that if humans have influence on land-cover composition, a larger influence would probably take place in the lowlands compared to the uplands of the study area. We counted the number of faeces from sheep, goats, donkeys, and cows, and noted whether cuttings of shrubs and/or trees had taken place in the quadrat to indicate the degree of browsing pressure and direct human impact, respectively.

The strength and statistical significance of species–environment relationships were analysed using the program CANOCO 4.5 (TER BRAAK 1987). Both data sets (2001 and 2005) were preliminarily analysed by detrended correspondence analysis (default settings) (DCA) (HILL and GAUCH 1980) to determine the length of the gradient, to test the homogeneity of the data, and to decide on which ordination analysis to apply. The length of gradient determined by DCA was > 2SD-units for the first axis, so we opted for the unimodal ordination technique, correspondence analysis (CA) with a biplot scaling (default settings), to provide an optimal weighted average approximation for biplot interpretation of species–environ-

²⁾ 'Grain' is the size of the individual units of observation, the plot size or the sample units (WIENS 1989; WHITTAKER et al. 2001).

Percentage cover	Abundance scale	
76–100% cover	7	
51–75% cover	6	
26-50% cover	5	
12.6 –25% cover	4	
6.26-12.5% cover	3	
< 6.25% cover	2	
Single, young individual	1	

ment relationships. The environmental factors were coded as follows: time as 1 and 5 (2001 and 2005), elevation as metres above sea level (m a.s.l.), human impact as a dummy variable (1/0), and browsing as log-transformed number of faeces in each quadrat. In addition we included species richness as total number of species (including herbs). The environmental variables were correlated with the CA axes. In addition, we performed a canonical correspondence analysis (CCA) to investigate changes in species related to time (2001 and 2005) and tested the significance of elevation, human impact, and faeces using a Monte Carlo permutation test with 999 permutations. CCA emphasises qualitative differences, thus we also did a Monte Carlo permutation test in redundancy analyses (RDA on a covariance matrix) that emphasise differences in abundance. The distribution of quadrats or species in the CA diagram indicates the degree of similarity between them: quadrats or species that are positioned close to each other in the diagram (see results section; Figs. 4 and 5) have a higher degree of similarity compared to quadrats or species positioned further apart.

3.3 Regeneration of important shrubs and trees using permanent plots along an elevational gradient

Permanent plots were used to investigate sprouting, growth, and survival of seedlings, juveniles, shrubs, and trees from 2003 to 2007. Six permanent plots of 25 m² each were positioned along a mountain slope to cover an elevational gradient (Fig. 1). Plant abundance was estimated by the same procedure as for the transects (Tab. 1). The shrub and tree canopy circumference and the position of the stump were drawn on a map, and all the species' heights were noted. Seedlings were defined as small plants with embryonic roots, embryonic shoots, and cotyledons (seed leaves). Juveniles were defined as perennial plants lower than 0.5 metres. Shrubs were defined as perennial plants lower than 2 metres, while trees were defined as perennial plants above 2 metres in height. We defined the division between shrubs and trees at the height of 2 metres, because this has been used in comparable studies in arid and semi-arid environments where trees are generally low (MURPHY and LUGO 1986; INRENA 1998; EKTVEDT 2003; HARPER et al. 2007). Vegetation surveys and mappings at fine scale were carried out four times during the period from 2003 to 2007. The first two surveys were carried out by the third author in February 2003 and November 2004, at the beginning of and during the rainy season. The two last surveys were carried out by the first author at the end of the rainy season in April 2005 and May 2007. The surveys were carried out in different seasons to contribute to the understanding of seasonal pulsation in the dry forest. The permanent plots are few, but detailed canopy cover estimates at a species level were done. Conclusions may not be drawn on the basis on these permanent plots, although trends may be implicated.

4 Results

4.1 Aerial photo interpretation

Interpretation of aerial photos from 1949, 1962, and 1999 (Fig. 3) indicates four main changes: (1) The total size of forest decreased by 16.6 % (359 ha) from 1949 to 1999, giving an annual decrease of 0.33%. From 1949 to 1962 total forest size showed a small decline, only 1.7% (37.2 ha), while forest size showed a proportionally larger decline of 14.9% during 1962 to 1999 (321.5 ha) (expected decline for the period given the previous rate of loss would have been 5.1%). (2) The total area of cultivated land increased by 321 ha. (3) The number of patches increased during the period of investigation: forest patches and cultivated patches increased almost threefold during the total period from 1949 to 1999. The largest increase in number of patches was from 1949-1962 (Tab. 2). Also plantation patches increased during the investigation period, with the largest increase in number of patches from 1949 to 1962 (Tab. 2). (4) The coverage of roads increased during the period, and both contributed to a fragmentation of land areas and eased access to them (Fig. 3).

To understand whether fragmentation has taken place, we investigated the number of kilometres of edges of forest patches from 1949 to 1999. In

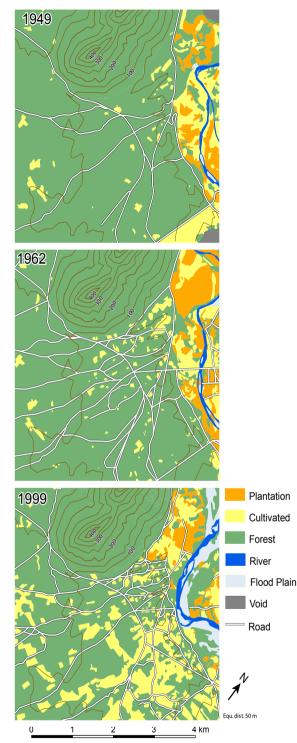


Fig. 3: Interpretation of land coverage in the study area in 1949, 1962, and 1999. Aerial photos from Servicio Aerofotográfico Nacional (SAN), and Instituto Geográfico Nacional (IGN), Lima, Peru

1949 the total perimeter of all forest patches was 121 km, while in 1962 the number had increased to 209 km. In 1999 the total perimeter of all forest patches was 242 km. The forest edges doubled during the 50-year period. Figure 3 shows the fragmentation of land cover areas, the decline of forest areas, and the increase in cultivated areas. At the bottom of the right-hand corner of the aerial photo from 1949 we see a larger patch classified as *culti*vated land. In 1962 the same patch is classified as forest (Fig. 3). This classification was made because we distinguished tiny stripes in a regular pattern in the patch from 1949, which could be interpreted as access paths for cultivation. In addition, no tree crowns were seen in this patch in the 1949 photo. However, tree crowns were clearly observed in an irregular pattern on the 1962 photo, and we interpreted this to be a forest pattern. In the photo from 1999 we see that the same patch developed into a mixture of both cultivated land and forest (Fig. 3).

4.2 Ordination results

The ordination analyses revealed both a spatial elevational gradient and a temporal gradient. Change in species composition along the spatial elevational gradient (lowland-upland) is represented by the first CA-axis (Fig. 4 and Fig. 5). Species richness increases with increasing elevation (Fig. 6) and shows a significant correlation (0.36) to the first CA-axis (Fig. 5). The second axis represents the temporal gradient (2001–2005). The CA analysis shows that the floristic composition of some quadrats changed only slightly from 2001 to 2005, whereas other quadrats experienced larger changes in species composition (Fig. 4). This spatio-temporal configuration is confirmed by correlations, where both *elevation* has a significant correlation with the first axis (0.59) and time has a weak correlation with the second axis (0.18) and a stronger correlation with the third axis (0.32) (Tab. 3). A Monte Carlo permutation test (999 permutations) in canonical correspondence analysis (CCA) revealed that temporal changes (time) as well as the spatial component elevation (m a.s.l.) were significant. The same test showed that logging (human impact) and browsing (represented by number of faeces) were not significantly correlated to any of the CCA-axes (Tab. 4). However, redundancy analvsis (RDA), which emphasises changes in species abundance more than qualitative changes of species composition, indicated that browsing (faeces) was a significant factor (Tab. 4).

	1949		1962		1999	
	Total ha	No. of patches	Total ha	No. of patches	Total ha	No. of patches
Forest	2164.4	37	127.2	107	1805.7	113
Cultivated	227.1	61	206.1	132	547.9	177
Plantation	115.7	24	192.5	51	92.3	34
River	23.9	1	26.3	3	35.7	1
Flood plain	10.1	8	16,8	31	98,6	40
Void	22.5	2	0	0	0	0
TOTAL	2563.7	133	2568.9	324	2580.2	364

Tab. 2: Total hectare (ha), number (nr) of patches for the categories lowland forest, bill forest, cultivated, plantation, river, flood plain and void in the years 1949, 1962 and 1999

Figure 5 depicts the position of species with respect to the temporal gradient and spatial elevational gradient. Species with a high score on axis two have increased in number and/or abundance from 2001 to 2005, whereas a negative score on axis two indicates a decrease in number and/or abundance from 2001 to 2005. Jacquemontia prominens (Jacq pro), Abutilon reflexum (Abut ref), Capparis scabrida tree (Capp sct), Cordia lutea tree (Cord lut), Prosopis pallida tree (Pros pat), Loxopteryogium huasango shrub (Loxo hus), Acacia macracantha tree (Acac mat) and Caesalpinia paipai tree (Caes pat) all have a higher degree of presence in 2001 than in 2005. Species that had a higher presence in 2005 compared to 2001 are Cordia lutea shrub (Cord lus), Ruellia floribunda (Ruel flo), Bursera graveolens tree (Burs grt), Lantana scabiosaeflora (Lant sca) and Prosopis pallida shrub (Pros pas). Two species, Ophryosporus peruvianus (Ophr per) and

Loxopterygium huasango (tree) (Laxo hut), seem to be outliers. They both had low frequency and the interpretation of their changes is not certain. *Prosopis pallida* dominates in the lowlands (Fig. 5).

4.3 Results of regeneration in permanent plots analyses

The canopy cover of shrubs and trees decreased in the period 2003–2007 at **low elevations** (110 m a.s.l.) (plots 1 and 2; Fig. 7). The number of shrubs and trees decreased, while juveniles increased from 2003–2007. No seedlings were found in 2003 and 2004, but seedlings were registered in 2005: thirty-five in plot 1 and thirteen in plot 2. Of these, 26.5% (plot 1) and 30% (plot 2) had developed to juveniles by 2007 (Fig. 7). All seedlings developed outside the canopy

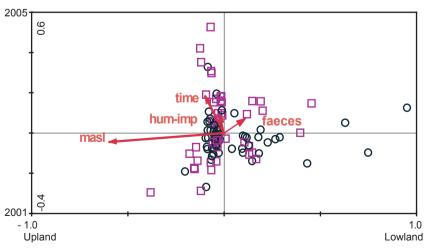


Fig. 4: Correspondence analysis showing the distribution of quadrats analysed in 2001 (circles) and 2005 (squares). The first axis is an elevation gradient (lowland-upland), while the second axis represents the time gradient (2001–2005). Environmental variables such as human impact (hum-imp), elevation (masl), number of species (spp-no), faeces, and time are shown

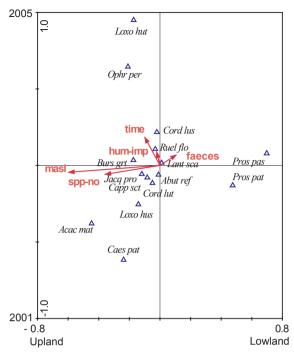


Fig. 5: Correspondence analysis of the species composition in relation to environmental variables such as human impact (hum-imp), elevation (masl), number of species (spp-no), faeces, and time are shown. The first axis is an elevation gradient (lowland–upland), while the second axis represents time (2001–2005)

coverage of other shrubs and trees. All species found at low elevations were *P. pallida* (except for one single *Acacia macracantha*).

The canopy cover of trees remained stable or decreased slightly at **mid elevations** (220 m a.s.l.) (plots 3 and 4; Figs. 7 and 8). None of the juveniles grew up to become shrubs in the period 2003–2007. An increasing number of species was seen at mid elevations: in addition to *P. pallida*, we also registered *Cordia lutea* (overal), *Caesalpinia paipai* (charán), and *Bursera graveolens* (palo santo). Seedlings were only present in 2005 and 2007. In 2005 seedlings of *B. graveolens*, *P. pallida*, and *C. paipai* were present, but none survived until 2007. However, seedlings of *C. lutea* appeared in 2007 (Figs. 7 and 8).

All trees and most shrubs at **high elevations** (380 m a.s.l.) (plots 5 and 6; Fig. 8) were stable over the period of investigation. The only juvenile individual (plot 5 in 2003 and 2004) did not survive in 2005. A large number of seedlings of *B. graveolens* were registered in plot 5 (55 seedlings) and plot 6 (107 seedlings) in 2003, but all had died by November 2004. In 2005 seedlings from several species (*A. macracantha, B. graveolens, C. paipai*, and *C. lutea*) appeared, but none survived until May 2007 (Fig. 8).

5 Discussion

The aerial photo interpretation revealed longterm land-cover change and showed that the forest decreased by ~17% over the last 50 years, giving an annual decline of 0.33%. The decrease in forest was probably caused by an increase in cultivated land. The number of patches increased most in the categories of *forest* and *cultivation*, indicating that these areas have decreased in plot size. The ordination analysis showed a change in species composition during the four-year investigation. The permanent plots were few but detailed, and indicated that *Prosopis pallida* was the only species that was able to survive from seedling to juvenile, whereas seedlings of all other species died during the four years of investigation.

5.1 Long-term land-cover change

This study is one of few studies with regard to land-cover change in dry tropical hardwood forest in northern Peru covering 50 years. This research has shown that dry forests in northern Peru are being transformed to agricultural land and that the average forest decline is 0.33% per year. Increased agricultural activities have been found to be one of the primary factors in deforestation and fragmentation in 96% of 152 tropical forests investigated, followed by wood extraction and infrastructure expansion (GEIST and LAMBIN 2002). Demographic, economic, technological, cultural, policy, and institutional factors are also considered to be underpinning causes of deforestation (e.g. GEIST and LAMBIN 2002; LAMBIN et al. 2003; CHAZDON 2003: MENA et al. 2006: KAIMOWITZ and ANGELSEN 2008). Increase in agricultural activities is the most likely reason for forest loss in northern Piura, since forest loss (359 ha) nearly corresponds to the increase in cultivated land (321 ha) during the 50-year period investigated. Our results are in accordance with other studies carried out in Peru which also demonstrate that forests are being transformed to agriculture (e.g. FAO 2010). The total deforestation rate in Peru from 1990 to 2000 was estimated by FAO (2001) to be 0.4% per year.

It is challenging to compare deforestation rates between studies because different classification systems, different frequencies, and assessment methods are often used when monitoring forests. Different forest definitions are used for different purposes and this makes global and continental forest estimates diverse (e.g. ALLEN and BARNES 1985). However, the FAO, in collaboration with countries and key partner organisations is currently undertaking a remote-sensing survey

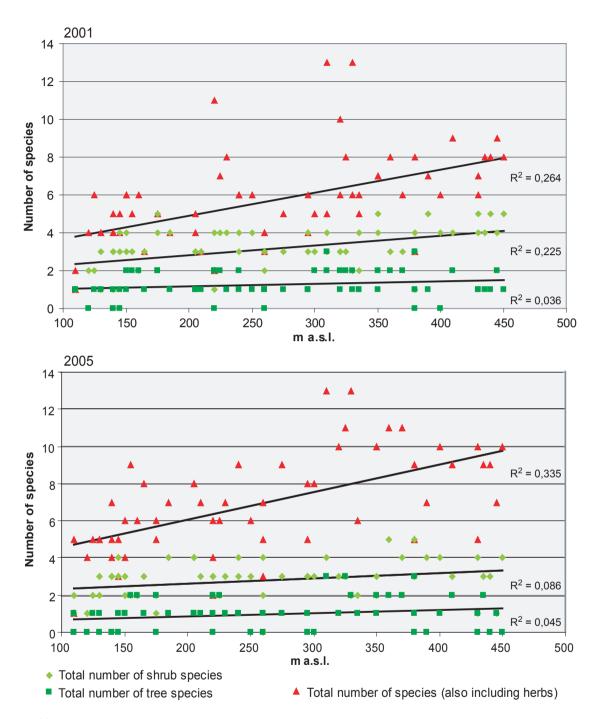


Fig. 6: Total number of shrubs, total number of trees, and total number of all species (including herbs) along the elevational gradient of the small forested mountain in 2001 and 2005. Total number of species (including herbs) increased from 2001 to 2005, and total number of species increases with increasing elevation. There was a quite stable level of trees from the lowland to the upland, while number of shrubs increased with elevation, but showed a decreasing trend from 2001 to 2005

of forests, sampling about 13,500 sites over a period of 15 years and this will provide more accurate data on global and regional rates of deforestation by the end of 2011 (FAO 2010). We found that during 1949–1962 forest loss was 'only' 1.7%, while during 1962–1999 forest loss was nearly three times greater (15% in total). Several possible factors can explain the increased forest loss seen

Tab. 3: Inter-set correlations of environmental variables with axes in the ordination analysis. Environmental variables are *faeces, elevation* (masl), *human impact* (hum-imp), and *time*. Number of species in each plot (spp-no) is correlated to see the spatial distribution of the richness gradient

Name	AX1	AX2	AX3	AX4
Eigenvalues	0.3305	0.2824	0.2650	0.2527
faeces	0.10	0.07	0.08	0.09
masl	-0.59	-0.04	-0.07	-0.33
hum-imp	-0.02	0.09	-0.04	-0.15
time	-0.10	0.18	0.32	0.14
spp-no	-0.36	-0.06	0.12	-0.02

on the aerial photos after 1962. One possible explanation is the agrarian land reform that took place in 1969. Before this reform, Peruvian land ownership structure was uneven: a small group of landowners (< 2%) owned more than 80% of the arable coastal land (HUDSON 1992). The land reform restructured this uneven division of land, and transferred ownership to the employees and workers (HUDSON 1992). This resulted in an increase in the number of landowners and more fragmented land.

Another possible explanation for increased forest loss during 1962–1999 may be due to population increase and thus a need to convert forest areas to agricultural land. In 1940 Piura district was the sixth most populated district in the country with 432,044 inhabitants (INEI 2003). In 1993 Piura had become the second most populated district, next to Lima, and in 2003 the total population size in Piura was 1,660,952 (INEI 2003).

A third possible explanation can be a change in poverty levels for the locals (and therefore greater dependence on forest resources for survival, or converting forest areas to agricultural land). The degree of poverty is measured by The Peruvian National Statistical Institute (INEI, www.inei.gob.pe) using two alternative measurements besides household income: the Unsatisfied Basic Needs (UBN) index and the caloric deficit (INEI 2005; JAPAN BANK FOR INTERNATIONAL COOPERATION 2007). Between May 2003 and April 2004, 62.6% of the population in Piura were considered poor, with 22% of these considered extremely poor (INEI 2005). In 2009 Piura department had decreased their level of poverty to 39.6% (no information on extreme poverty) (INEI³). A reduction in poverty level of 23% in

nine years seems dramatic. A plausible explanation for this is that the methods used to measure poverty have changed several times (THE WORLD BANK 2008) and this has resulted in questions about the quality of the statistics and criticism of INEI for not presenting transparent statistics (e.g. SALAZAR 2008; MATUK 2011; LARREA 2011). However, if it is correct that poverty has decreased in Piura in recent times, it exemplifies that the land reform, and the subsequent transformation of forest to agriculture land has had a delayed but positive impact on human welfare in the study area.

This change has also resulted in more fragmentation during the last 50 years. The effect of fragmentation on forest dynamics is that species composition may be modified and single species may be threatened, as found in other tropical forests where human interaction took place (e.g. GUARIGUATA and DUPUY 1997; ECHEVERRÍA et al. 2007), depending on the size of the patch, its species composition, and its degree of isolation. If the distances between similar plots are small, spreading of plants from one plot to the next can still take place (FARINA 2006). Prosopis pallida was the dominant species in the lowland area, and can easily spread even if a 'road' divides a forest area, and may not suffer from fragmentation caused by 'roads' as defined in this study. However, other species may suffer from this kind of fragmentation, but a negative relationship between species richness and fragmentation in tropical forests used by humans is not always supported (FAUDE et al. 2010).

5.2 Short-term vegetation change

The ordination analysis indicates a clear spatial elevational gradient in both species composition and species richness (Fig. 5 and 6). The latter increases with elevation, which has been demonstrated in many studies, and it has been correlated to change in climate along the elevational gradient (BARUCH 2005; BHATTARAI and VETAAS 2003). The average temperature decreases by 6.49 °C/1000 m based on the Environmental Lapse Rate (ELR) which is the international standard value set by the International Civil Aviation Organization (ICAO) (ICAO, 2002). The difference in elevation at our study site is 350 metres, indicating a temperature difference of 2.3 °C between the lowland and upland of the forested moun-

³⁾ Source: www.inei.gob.pe (accessed August 2011): 'Información Social', 'Perfil de la pobreza 2005–2009', '2 – Incidencia de la Pobreza en el 2009', 'Perú: Incidencia de la

pobreza, según departamentos, 2008 y 2009', Piura = 39.6% (2009). Statistic source: INEI – Encuesta Nacional de Hogares (ENAHO), Anual 2008 y 2009.

Plot 1 Plot 3 Plot 2 220 m a.s.l. 110 m a.s.l. 110 m a.s.l. Species: Species: Species: Prosopis pallida 'algarrobo' Prosopis pallida 'algarrobo' . Prosopis pallida 'algarrobo' Acacia macracantha (Am) 'faique' Cordia lutea (Cl) 'overal' Seedlings: Seedlings: Bursera graveolens (Bg) 'palo santo' Prosopis pallida 'algarrobo' Cordia lutea (Cl) ' overal' Prosopis pallida 'algarrobo' Caesalpinia paipai (Cp) 'charán' 1.60 5.00 •1 d February 18, 2003 0.60 €/•2.58 €/•1.80 2.30 .24 • 0.26 • 0.76 0.80 .2.0 • **0**,50 V .30 0.83 .42 CI • 2. CI . 2.55 230 5.50 •1 November 25, 2004 0.72 Cl • 3.50 1.7 0.300.77 1.30 155 .26 .90 CI•-CI • 2.74 4.50 .* 1. •1.50 0.15 .2.00 April 18, 2005 •1.00 .0 · 2.00 , × ' 127 •1 40 • 0.26 CI 2.22 × CI •2.2 1.80 **5**.50 0.90 0.7 €/•1.50 €/•3.50 •2.55 May 20, 2007 0.110.12 0.10 0.10 0.10 0.15 0.1200.10 •^{0.15}••^{0.30} 0.20 к Cl ∗ Cl Cll• 2.50 or Permanent plot Juveniles, trees or shrubs. X Seedlings, Am • c/ • 3.00 5x5 meters Dots indicate position of trunk. 1.40 letters next to cross Number is height, letters indicate species indicate species Juveniles (under 0.5 meters in height) Shrubs (0.5 - 1.99 meters in height) Trees (2 meters in height or more)

Fig. 7: Permanent plots at 110 m a.s.l. (plots 1 and 2) and 220 m a.s.l. (plot 3). Each species is marked with the first two letters of the species name. Those without a symbol are *Prosopis pallida* (due to abundance). Species height (in metres) is given next to the root

Plot 6

380 m a.s.l.

Plot 5

380 m a.s.l.

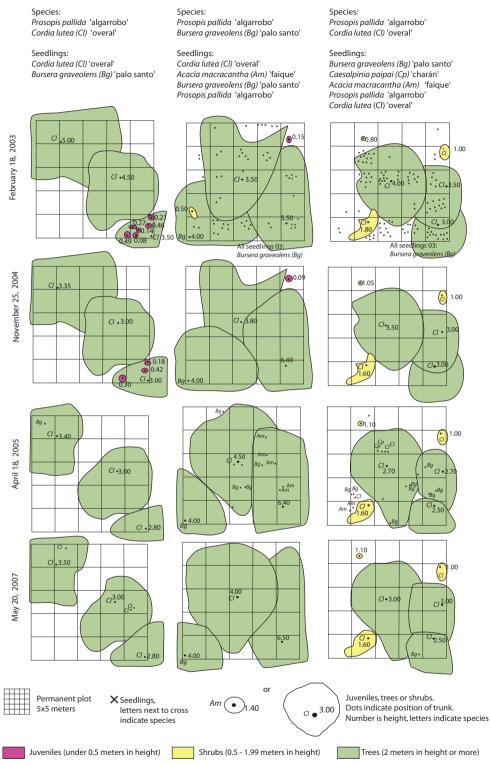


Fig. 8: Permanent plots at 220 m a.s.l. (plot 4) and 380 m a.s.l. (plots 5 and 6). Each species is marked with the first two letters of the species name. Those without a symbol are *Prosopis pallida* (due to abundance). Species height (in metres) is given next to the root

Plot 4

220 m a.s.l.

CCA-analysis		RDA -analysis	
F-value	P-value	F-value	P-value
8.6	0.001	15.0	0.001
8.2	0.001	8.7	0.001
0.5	0.9 (ns)	2.3	0.026
1.0	0.42 (ns)	0.3	0.98 (ns)
	F-value 8.6 8.2 0.5	F-value P-value 8.6 0.001 8.2 0.001 0.5 0.9 (ns)	F-value P-value F-value 8.6 0.001 15.0 8.2 0.001 8.7 0.5 0.9 (ns) 2.3

Tab. 4: Unrestricted Monte Carlo Permutation Test with 999 permutations with the CCA and RDA analyses

tain. This may create a higher degree of moisture at higher elevations compared to the lowland area due to reduced evapotranspiration resulting in a higher number of species than would be expected (O'BRIEN 2006). This has been documented for similar forests in South America (BARUCH 2005).

As mentioned in the method section, a small inaccuracy in our surveying while sampling could occasionally have occurred, since we registered some perennial plants in 2005 that were absent in the 2001 analysis. However, Ross et al. (2010) addressed whether relocation uncertainty can affect the validity of the results by re-measuring a 50-yearold study, where original geographical coordinates were relocated to the nearest 100 m x 100 m and plot size was 4 m². The authors concluded that even though the original plots cannot be exactly relocated within the vegetation stand, reliable changes in species composition are still possible to detect (Ross et al. 2010). In several other studies considering revisiting plots, only some selected plots have been re-measured (Ross et al. 2010). In this study all the plots were re-measured, minimizing the risk of random noise (Ross et al. 2010).

The long-term investigation (50 years) found increased agricultural and decreased forest cover that may have influenced species composition in the area as demonstrated in other tropical forests (e.g. ECHEVERRÍA et al. 2007). The ordination analysis indicates a weak, but significant change in species composition with time. However, the ordination analysis did not reveal a significant relationship between species composition and human impact or faeces, but a Monte Carlo permutation test in RDA (emphasis on difference in abundance) revealed a significant effect of *faeces* on species composition. Several studies have shown that human interaction can change species diversity and abundance in tropical dry forest environments (VETAAS 1993; GILLESPIE et al. 2000; RICHTER and ISE 2005; GWALI et al. 2009). Human impact and browsing are challenging to measure, especially on a small species matrix. The method used in this investigation may not be able to capture human impact satisfac-

torily, probably because consumption of forest resources and browsing takes place quite evenly over the entire study area, rather than being restricted to a certain area. It is easier to demonstrate the effect of human impact when plots with easy human access have less species diversity and abundance than plots with difficult human access (GWALI et al. 2009). Thus we hypothesise that browsing may have an effect on species composition, but further investigations are necessary to test this empirically. The investigation of permanent plots revealed that seedlings emerged after precipitation events in 2003, 2005, and 2007. Only seedlings of Prosopis pallida survived from seedling stage to juvenile stage (survival rate of about 30%). The amount of precipitation from the beginning of the rainy period to the survey each year did not exceed 120 mm in Chulucanas (PROYECTO ESPECIAL CHIRA-PIURA⁴), indicating that most of the species need higher precipitation rates to survive from seedling to juvenile stages, which has been demonstrated along the coastal desert of northern Chile (SCHULZ et al. 2011). Bursera graveolens, Acacia macracantha, Caesakoaunia paipai, and Cordia lutea had a high death rate of seedlings during the survey period, which is common in arid and semi-arid forests (HALL et al. 1964; GERHARDT 1996). A high death rate of Bursera graveolens (HAMMAN 2001; LINARES-PALOMINO and Ponce Alvarez 2005) and Acacia macracantha (RICHTER 2005) have previously been found in similar environments. The permanent plots and the gradient analyses revealed that recovery of plant cover and spatio-temporal trends in species composition in dry lands is strongly controlled by water availability (HOLMGREN 2008; CHESSON et al. 2004; ZEMMRICH 2007; SCHULZ et al. 2011).

⁴⁾ Monthly precipitation data from Chulucanas climate station (05°06'12'', 80°09'57''), Proyecto Especial Chira-Piura (PECHP); http://www.chirapiura.gob.pe/principal. php. From the beginning of the rainy period until vegetation registration that year, it rained: October 2002–February 2003 = 99.1 mm. From September 2003–November 2004 = 6.1 mm. From September 2004–April 2005 = 117.0 mm. From November 2006–May 2007 = 84.3 mm.

6 Conclusions

This study is one of few studies on semi-arid forests in northern Peru and has documented forest loss over the last 50 years. From 1949 to 1999, the size of forest declined by ~17%, corresponding to an average forest decline of 0.33% annually. The forest degradation during the 50 years in northern Peru was mainly due to agricultural expansion, as also seen in many other studies. Forest declined about 1.7% during 1949-1962, while a greater forest decline of 15% was seen during 1962-1999. A new agrarian land reform in 1969 and population increases are likely reasons for the transformation of forest to agriculture land and an increase in number of patches in the period from 1962–1999, which may be the underpinning reason for a reduced poverty level in the area. On a finer scale of resolution we found a significant difference in species composition between the two years (2001 and 2005) of sampling, and we hypothesise that this may relate to browsing, but the statistical tests were not equivocal. The change in species richness and species composition with elevation may be due to climatic differences between the lowland and upland mountain study area, rather than the different intensity of human land use. The seedling monitoring in the permanent plots (2003 to 2007) revealed that about 30% of the Prosopis pallida seedlings developed into juveniles, but all other seedlings died. This species may be better adapted to drought than other species

in this environment, and other species may need higher amounts of precipitation than that which fell during 2003 to 2007. The knowledge gained from this study may be important for future causal studies on the driving forces in dry forests found in a matrix of agriculture land.

Acknowledgements

We thank Luis Urbina (botany student at Universidad de Piura, Peru) and Luis Alban Contreras (Administrative Director at Nature and Culture International, Peru) for field assistance and plant identification. We also thank Freddy Zuñinga Varillas (Professor of Biology, Universidad Nacional de Piura, Peru) and Maria Isabel La Torre Acuy, Severo Balderón, and Hamilton Beltran (all botanists at Museo de Historia Natural, Lima) for identification of plants. Grover Otero (PECHP) and Hector Yuari Quispe (SENHAMI) were contact persons for obtaining climate data. The late Tore Borvik assisted in the preparation of aerial photos and Kjell Helge Sjøstrøm gave guidance on improving the layout of Figs. 1, 3, 7, and 8. We also thank Kerstin Potthoff, Gunilla Almered Olsson and Achim Bräuning for discussion of issues, as well as two anonymous referees for helpful comments. Cathy Jenks corrected language errors. This research was financed by the Norwegian Research Council (to T.M.E., (166045/V10)).

Ν	Shortening	Scientific name	Axis 1 scores
1	Pros pas	Prosopis pallida (shrub)	2,3447
2	Pros pat	Prosopis pallida (tree)	1,5974
15	Lant sca	Lantana scabiosaeflora HBKK	0,0369
12	Abut ref	Abutilon reflexum	-0,0336
4	Cord lus	<i>Cordia lutea</i> (shrub)	-0,0687
11	Ruel flo	Ruellia floribunda	-0,1027
5	Cord lut	Cordia lutea (tree)	-0,1648
10	Capp sct	Capparis scabrida (tree)	-0,2784
13	Jacq pro	Jacquemontia prominens	-0,3989
6	Loxo hus	Loxopteryogium huasango (shrub)	-0,4748
7	Loxo hut	Loxopteryogium huasango (tree)	-0,5778
8	Burs grt	Bursera graveolens (tree)	-0,5841
14	Ophr per	Ophryosporus peruvianus	-0,7039
9	Caes pat	<i>Caesalpinia paipai</i> (tree)	-0,7985
3	Acac mat	Acacia macracantha	-1,5032

Appendix 1: Species scores (biplot scaling) ranged after axis 1 scores

References

ALLEN, J. and BARNES, D. E. (1985): The causes of deforestation in developing countries. In: Annals of the Association of American Geographers 75, 163–184. DOI: 10.1111/j.1467-8306.1985.tb00079.x

- ARMESTO, J. A.; VIDIELLA, P. E. and GUTIÉRREZ, J. R. (1993): Plant communities of the fog-free coastal desert of Chile: plant strategies in a fluctuating environment. In: Revista Chilena de Historia Natural 66, 271–282.
- BARUCH, Z. (2005): Vegetation-environment relationships and classification of the seasonal savannas in Venezuela. In: Flora 200, 49–64. DOI: 10.1016/j.flora.2004.06.001
- BEHNKE, R. H.; SCOONES, I. and KERVEN, C. (eds.) (1993): Range ecology at disequilibrium. London.
- BENDIX, J.; TRACHTE, K.; PALACIOS, E.; ROLLENBECK, R.; GÖTTLICHER, D.; NAUSS, T. and BENDIX, A. (2011): El Niño meets La Niña – Anomalous rainfall patterns in the "traditional" El Niño region of Southern Ecuador. In: Erdkunde 65, 151–167. DOI: 10.3112/erdkunde2011.02.04
- BHATTARAI, K. R. and VETAAS, O. R. (2003): Variation in plant species richness of different lifeforms along a subtropical elevation gradient in the Himalayas, east Nepal. In: Global Ecology and Biogeography 12, 327– 340. DOI: 10.1046/j.1466-822X.2003.00044.x
- BLOCK, M. and RICHTER, M. (2000): Impacts of heavy rainfall in El Niño 1997/98 on the vegetation of Sechura Desert in Northern Peru. A preliminary report. In: Phytoeconologia 30 (3-4), 491–517.
- CABREJOS VÁSQUEZ, C. M.; GRADOS QUESADA, N.; ALBÁN CONTRERAS, L. and SÁNCHEZ MONTOYA, M. (2006): Fuentes semilleras – una oportunidad para el desarrollo sostenible local [The sources of the seeds – a possibility for local sustainable development]. Universidad de Piura and Centro Ideas Programa Piura. Piura, Perú.
- CHAZDON, R. L. (2003): Tropical forest recovery: legacies of human impact and natural disturbances. In: Perspectives in Plant Ecology, Evolution and Systematics 6, 51–71. DOI: 10.1078/1433-8319-00042
- CHESSON, P.; GEBAUER, R. L. E.; SCHWINNING, S.; HUNTLY, N.; WIEGAND, K.; ERNEST, M. S. K.; SHER, A.; NOVOP-LANSKY, A. and WELTZIN, J. F. (2004): Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. In: Oecologia 141, 236– 253. DOI: 10.1007/s00442-004-1551-1
- CONGRESO DE LA REPÚBLICA DEL PERÚ (2000): Ley Forestal y Fauna Silvestre N° 27308. Reglamente de la ley Forestal. Promulgada el 15. Julio 2000. Publicada el 16. Julio 2000. DS.014-2001-AG. [The law of forest and wild fauna N° 27308. The regulation of the forest law. Notification the 16th of July 2000. DS.014-2001-AG]. Congreso de la república del Perú, Lima.

- CONDIT, R.; HUBBELL, S. P. and FOSTER, R. B. (1996): Changes in tree species abundance in a Neotropical forest: impact of climate change. In: Journal of Tropical Ecology 12, 231–256. DOI: 10.1017/S0266467400009433
- COTLER, H. and MAASS, J. M. (1999): Tree management in the northwestern Andean Cordillera of Peru. In: Mountain Research and Development 19, 153–160. DOI: 10.2307/3674256
- DILLON, M. O. and RUNDEL, P. W. (1990): The botanical response of the Atacama and Peruvian Desert floras to the 1982-83 El Niño event. In: GLYNN, P. W. (ed.): Global ecological consequences of the 1982-83 El Niño Southern Oscillation. Cambridge, 487–504.
- ECHEVERRÍA, C.; NEWTON, A. C.; LARA, A.; REY BENAYAS, J. M. and COOMES, D. A. (2007): Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. In: Global Ecology and Biogeography 16, 426–239. DOI: 10.1111/j.1466-8238.2007.00311.x
- EKTVEDT, T. M. (2003): Vegetasjonsdynamikk i Piura (Peru) før og etter El Niño-hendelsen 1997/98. En undersøkelse av stabilitet og endring i vegetasjonen [Vegetation dynamics in Piura (Peru) before and after the El-Niñoevent of 1997/98. An investigation of stability and change in the vegetation]. Master thesis. Bergen (in Norwegian)
- (2011): Firewood consumption amongst poor inhabitants in a semiarid tropical forest: A case study from Piura, northern Peru. In: Norwegian Journal of Geography 65, 28–41. DOI: 10.1080/00291951.2010.549951
- FARINA, A. (2006): Principles and methods in landscape ecology: toward a science of landscape. Dordrecht.
- FAUDE, U.; FEILHAUER, H. and SCHMIDTLEIN, S. (2010): Estimating the impact of forest use on biodiversity in protected areas of developing tropical regions. In: Erdkunde 64, 47–56. DOI: 10.3112/erdkunde.2010.01.04
- FERREYRA, R. (1993): Registros de la vegetación en la costa Peruviana en relación con el fenómeno El Niño [Registration of the Peruvian coast vegetation in relation to the El Niño phenomenon]. In: Bulletin de l'Institut Français d'Études Andines 22, 259–266.
- FAO (FOOD and AGRICULTURE ORGANIZATION). (2001): Global Forest Resources Assessment 2000. FAO Forestry Paper 140. Rome, 279–291. http://www. fao.org/icatalog/search/dett.asp?aries_id=102270 (accessed May 2010).
- (2005): Global Forest Resources Assessment 2005. Rome.
- (2006): Choosing a forest definition for the Clean Development Mechanism. Forests and Climate Change Working Paper 4, Rome.
- (2010): Global Forest Resources Assessment 2010. Main report. Rome. http://www.fao.org/forestry/fra2010 (accessed January 2011).

- FURLEY, P.; GRACE, J. and MEIR, P. (2006): Tropical savannas and seasonally dry forest: an introduction. In: Journal of Biogeography 33, 385–386. DOI: 10.1111/j.1365-2699.2005.01471.x
- GEIST, H. J. and LAMBIN, E. F. (2002): Proximate causes and underlying driving forces of tropical deforestation. In: BioScience 52, 143–150. DOI: 10.1641/0006-3568(2002)052[0143:PCAUDF]2.0.CO;2
- GERHARDT, K. (1996): Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. In: Forest Ecology and Management 82, 33–48. DOI: 10.1016/0378-1127(95)03700-4
- GILLESPIE, T.; GRIJALVA, A. and FARRIS, C. N. (2000): Diversity, composition, and structure of tropical dry forests in Central America. In: Plant Ecology 147, 37–47. DOI: 10.1023/A:1009848525399
- GOLDBERG, R. A.; TISNADP, M. and SCOFIELD, R. A. (1987): Characteristics of extreme rainfall events in Northwestern Peru during the 1982–1983 El Niño period. In: Journal of Geophysical Research 92, 14225–14241. DOI: 10.1029/JC092iC13p14225
- GUARIGUATA, M. R. and DUPUY, J. M. (1997): Forest regeneration in abandoned logging Roads in lowland Costa Rica. In: Biotropica 29, 15-28. DOI: 10.1111/j.1744-7429.1997.tb00002.x
- GUTIÉRREZ, J. R.; MESERVE, P. L; JAKSIC, F. M.; CONTRERAS, L. C.; HERRERA, S. and VÁSQUEZ, H. (1993): Structure and dynamics of vegetation in a Chilean arid thornscrub community. In: Acta Oecologica 14, 271–285.
- GUTIÉRREZ, J. R.; ARANCIO, G. and JAKSIC, F. M. (2000): Variation in vegetation and seed bank in a Chilean semiarid community affected by ENSO 1997. In: Journal of Vegetation Science 11, 641–648. DOI: 10.2307/3236571
- GWALI, S.; OKULLO, P.; HAFASHIMANA, D. and BYABASHIJA, D. M. (2009): Diversity and composition of trees and shrubs in Kasagala forest: a semiarid savannah woodland in central Uganda. In: African Journal of Ecology 48, 111–118. DOI: 10.1111/j.1365-2028.2009.01090.x
- HALL, E. A.; SPECHT, R. L. and EARDLEY, C. M. (1964): Regeneration of the vegetation on Koonamore vegetation reserve, 1926–1962. In: Australian Journal of Botany 12, 205–264. DOI: 10.1071/BT9640205
- HALVORSEN ØKLAND, R. (2002): Gradient analysis. Lecture notes 2002 update. Compendium. Museum of Botany. University of Oslo, Norway.
- HAMANN, O. (1985): The El Niño influence on the Galapagos vegetation. In: ROBINSON, G. and EL PINO, E. M. (eds.): El Niño en las Islas Galápagos: el evento de 1982–1983. Fundación Charles Darwin para las Islas Galápagos. Quito, 290–330.
- (2001): Demographic studies of three indigenous standforming plant taxa (*Scalesia*, *Opuntia* and *Bursera*) in the

Galápagos Islands, Ecuador. In: Biodiversity and Conservation 10, 223–250. DOI: 10.1023/A:1008952319105

- HARPER, G. J.; STEININGER, M. K.; TUCKER, C. J.; JUHN, D. and HAWKINS, F. (2007): Fifty years of deforestation and forest fragmentation in Madagascar. In: Environmental Conservation 34, 325–333. DOI: 10.1017/ S0376892907004262
- HILL, M. O. and GAUCH, H. G. (1980): Detrended correspondence analysis: an improved ordination technique. In: Vegetatio 42, 47–58. DOI: 10.1007/BF00048870
- HOLMGREN, M. (2008): Dryland dynamics and restoration: perspectives for the use of climatic swings. In: HOBBS, R. J. and SUDING, K. N. (eds): New models for ecosystem dynamics and restoration. The science and practice of ecological restoration. Washington D.C., 112–123.
- HOLMGREN, M.; STAPP, P.; DICKMAN, C. R.; GRACIA, C.; GRA-HAM, S.; GUTIÉRREZ, J. R.; HICE, C.; JAKSIC, F.; KELT, D. A.; LETNIC, M.; LIMA, M.; LÓPEZ, B. C.; MESERVE, P. L.; MILSTEAD, W. B.; POLIS, G. A.; PREVITALI, M. A.; RICHTER, M.; SABATÉ, S. and SQUEO, F. A. (2006a): Extreme climatic events shape arid and semiarid ecosystems. Reviews. In: Frontiers in Ecology and the Environment 4, 87–95. DOI: 10.1890/1540-9295(2006)004[0087:ECESAA]2.0.CO;2
- (2006b): A synthesis of ENSO effects on drylands in Australia, North America and South America. In: Advances in Geosciences 6, 69–72.
- HUDSON, R. A. (ed.) (1992): Peru: A country study. Chapter: 'People, Poverty and Farming'. GPO for the library of Congress. Washington. Also available at: http://countrystudies.us/peru/ (accessed August 2011).
- ICAO (INTERNATIONAL CIVIL AVIATION ORGANI-ZATION) (2002): Manual of the ICAO Standard Atmosphere (extended to 80 kilometres (262 500 feet)) (Doc 7488). Montreal, Canada.
- INEI (INSTITUTO NACIONAL DE ESTADISTICA E IN-FORMATICA) (2003): Almanaque Estadustico de Piura 2003. [Estatistical almanac for Piura 2003: Piura]. Lima, Peru.
- (2005): Condiciones de Vida en los Departementos del Peru: 2003-2004. [Living conditions for Peruvians departments: 2003-2004]. Lima, Peru.
- INRENA (INSTITUTO NACIONAL DE RECURSOS NA-TURALES) (1998): Mapa de bosques secos del Departamento de Piura. Memoria Descriptiva [Map of dry forest areas in the Piura district. A description]. Lima.
- JANZEN, D. H. (1988): Tropical dry forests: the most endangered major tropical ecosystems. In: WILSON, E. O. (ed.): Biodiversity. Washington D.C., 130–137.
- JAPAN BANK FOR INTERNATIONAL COOPERATION (2007): Poverty profile Peru (Executive Summary). Also available at:

http://www.jica.go.jp/activities/issues/poverty/profile/pdf/peru_e.pdf (accessed September 2011).

- KAIMOWITZ, D. and ANGELSEN, A. (2008): Will livestock intensification help save Latin America's forests? In: Journal of Sustainable Forestry 27, 6–24. DOI: 10.1080/10549810802225168
- KENT, M. and COKER, P. (1992): Vegetation description and analysis. A practical approach. London.
- LAMBIN, E. F.; GEIST, H. J. and LEPERS, E. (2003): Dynamics of land-use and land-cover change in tropical regions. In: Annual Review of Environment and Resources 28, 205– 241. DOI: 10.1146/annurev.energy.28.050302.105459
- LARREA, E. (2011): Cifras de crecimiento son infladas [The numbers of growth are inflated]. In: La República, June 20, 2011. Also available at: http://29x55.wordpress. com/ (accessed September 2011).
- LINARES-PALOMINO, R. and PONCE ALVAREZ, S. I. (2005): Tree community patterns in seasonally dry tropical forests in the Cerros de Amotape Cordillera, Tumbes, Peru. In: Forest Ecology and Management 209, 261–272. DOI: 10.1016/j.foreco.2005.02.003
- MATUK, F. (2011): Peru 2010: el mapa del hambre. [Peru 2010: the map of hunger]. In: La República, September 18, 2011. Also available at: http://29x55.wordpress. com/ (accessed September 2011).
- MENA, C. F.; BILSBORROW, R. E. and MCCLAIN M. E. (2006): Socioeconomic drivers of deforestation in the northern Ecuadoran Amazon. In: Environmental management 37, 802–815. DOI: 10.1007/s00267-003-0230-z
- MILES, L.; NEWTON, A. C.; DEFRIES, R. S.; RAVILIOUS, C.; MAY, I.; BLYTH, S.; KAPOS, V. and GORDON, J. E. (2006): A global overview of the conservation status of tropical dry forests. In: Journal of Biogeography 33, 491– 505. DOI: 10.1111/j.1365-2699.2005.01424.x
- MURPHY, P. G. and LuGO, A. E. (1986): Ecology of tropical dry forest. In: Annual Review of Ecology and Systematics 17, 67–88. DOI: 10.1146/annurev. es.17.110186.000435
- NILSSON, C. and GRELSSON, G. (1995): The fragility of ecosystems: a review. In: Journal of Applied Ecology 32, 677–692. DOI: 10.2307/2404808
- NOY-MEIR, I. (1973): Desert ecosystems: environment and producers. In: Annual Review of Ecology and Systematics 4, 25–51. DOI: 10.1146/annurev. es.04.110173.000325
- O'BRIEN, E. M. (2006): Biological relativity to water–energy dynamics. In: Journal of Biogeography 33, 1868–1888. DOI: 10.1111/j.1365-2699.2006.01534.x
- PENNINGTON, T. R.; LEWIS, G. P. and RATTER, J. A. (2006): An overview of plant diversity, biogeography and conservation of Neotropical savannas and seasonally dry forest. In: PENNINGTON, T. R.; LEWIS, G. P. and RAT-TER, J. A. (eds): Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation. Boca Raton, 1–29.

- RICHTER, M. (2005): Vegetation development before, during, and after El Niño 1997/98 in Northwestern Peru. In: Lyonia 8, 19–27.
- RICHTER, M. and ISE, M. (2005): Monitoring plant development after El Niño 1997/98 in northwestern Perú. In: Erdkunde 59, 136–155. DOI: 10.3112/erdkunde.2005.02.05
- Ross, L. C.; WOODIN, S. J.; HESTER, A.; THOMPSON; D. B. A. and BIRKS, H. J. B. (2010): How important is plot relocation accuracy when interpreting re-visitation studies of vegetation change? In: Plant Ecology & Diversity 3, 1–8. DOI: 10.1080/17550871003706233
- SALAZAR, M. (2008): Upbeat poverty stats questioned. InterPress Service, available at: http://www.ipsnews.net/ news.asp?idnews=42586 (accessed September 2011).
- SANKRAN, M.; HANAN, N. P.; SCHOLES; R. J.; JAYASHREE, R.;
 AGUSTINE, D. J.; CADE, B. S.; GIGNOUX, J.; HIGGINS, S.
 I.; LE ROUX, X.; LUDWIG, F.; ARDO, J.; BANYIKWA, F.;
 BRONN, A.; BUCINI, G.; CAYLOR; K. K.; COUGHENOUR, M.
 B.; DIOUF, A.; EKAYA, W.; FERAL, C. J.; FEBRUARY, E. C.;
 FROST, P. G.; HIERNAUX, P.; HRABAR, H.; METZGER, K. L.;
 PRINS; H. H.; RINGROSE, S.; SEA, W.; TEWS, J.; WORDEN, J.
 and ZAMBATIS, N. (2005): Determinants of woody cover
 in African savannas. In: Nature 438, 846–849. DOI: 10.1038/nature04070
- SCHOLES, R. J. and ARCHER, S. R. (1997): Tree–grass interactions in savannas. In: Annual Review of Ecology and Systematics 28, 517–544. DOI: 10.1146/annurev.ecolsys.28.1.517
- SCHULZ, N.; ACEITUNO, P. and RICHTER, M. (2011): Phytogeographic divisions, climate change and plant dieback along the coastal desert of Northern Chile. In: Erdkunde 65, 169–187. DOI: 10.3112/erdkunde.2011.02.05
- SCHWINNING, S.; SALA, O. E.; LOIK, M. E. and EHLERINGER, J. R. (2004): Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. In: Oecologia 141, 191–193. DOI: 10.1007/s00442-004-1683-3
- SHMIDA, A. (1985): Biogeography of the desert flora. In: EVENARI, M.; NOY-MEIR, I. and GOODALL, D. W. (eds.):. Ecosystems of the world 12A. Hot deserts and arid shrublands. Amsterdam, 23–77.
- SOTO, R. (1985): Efectos del fenómeno El Niño 1982–83 en ecosistemas de la I Región [El Niño 1982–83 effects on ecosystems' in the I Region]. In: Investigación pesquera (Chile) 32, 199–206.
- TER BRAAK, C. J. F. (1987): CANOCO a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). ITI-TNO. Wageningen.
- THE WORLD BANK/BANCO MUNDIAL (2008): Una mirada a la evolución reciente de la pobreza en el Peru:

avances y desafíos [A review of the late development of poverty in Peru: advances and challenges]. Washington DC.

- TRASS, H. and MALMER, N. (1973): North European approaches to classification. In: WHITTAKER, R. H. (ed.): Handbook of vegetation science. Part 5: Ordination and classification of vegetation. The Hague, 529–574.
- VETAAS, O. R. (1993): Spatial and temporal vegetation changes along a moisture gradient in northeastern Sudan. In: Biotropica 25, 164–175. DOI: 10.2307/2389180
- (2006): Biological relativity to water-energy dynamics: a potential unifying theory? In: Journal of Biogeography 33,1866–1867. DOI: 10.1111/j.1365-2699.2006.01618.x
- WELTZIN, J. E. and TISSUE, D. T. (2003): Resource pulses in arid environments – patterns of rain, patterns of life. In: New Phytologist 157, 167–173. DOI: 10.1046/j.1469-8137.2003.00672.x
- WHITTAKER, R. J.; WILLIS; K. J. and FIELD, R. (2001): Scale and species richness: towards a general, hierarchical theory of species diversity. In: Journal of Biogeography 28, 453–470. DOI: 10.1046/j.1365-2699.2001.00563.x
- WIEGAND, T. and JELTSCH, F. (2000): Long-term dynamics in arid and semiarid ecosystems – synthesis of a workshop. In: Plant Ecology 150, 3–6. DOI: 10.1023/A:1026552305348
- WIENS, J. A. (1989): Spatial scaling in ecology. In: Functional Ecology 3, 385–397. DOI: 10.2307/2389612
- ZEMMRICH, A. (2007): Equilibrium or non-equilibrium ecosystems? Scaling effects in rangeland ecosystems of Western Mongolia. In: Erdkunde 61, 335–343. DOI: 10.3112/erdkunde.2007.04.04

Authors

Tone Marie Ektvedt Ole Reidar Vetaas Anders Lundberg Department of Geography University of Bergen Fosswinckelsgate 6 5007 Bergen Norway tone.ektvedt@geog.uib.no ole.vetaas@geog.uib.no anders.lundberg@geog.uib.no