

WOODY VEGETATION OF A PERUVIAN TROPICAL DRY FOREST ALONG A CLIMATIC GRADIENT DEPENDS MORE ON SOIL THAN ANNUAL PRECIPITATION

JANNES MUENCHOW, HENRIK VON WEHRDEN, ERIC FRANK RODRÍGUEZ, RODOLFO ARISMÉNDIZ RODRÍGUEZ, FABIAN BAYER and MICHAEL RICHTER

With 3 figures and 1 table

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Summary: Tropical dry forests are the most threatened ecosystem in the tropics. Tropical dry forests possess an outstanding beta diversity, which can live up to rain forests standards, yet they are still vastly understudied. In northern Peru, El Niño Southern Oscillation (ENSO) fundamentally shapes these unique and highly endemic ecosystems. The objective of this study was to determine (i) if a main gradient was detectable in the woody plant composition in this hyper- to semi-arid environment; and (ii) to which extent climatic and edaphic variables account for it. Sampling was done on 50 30 × 30 m² random plots along a humidity gradient. A sodium-soil texture gradient correlated with the first Isomap axis. Potassium and pH, mainly representing precipitation, characterized the second axis. A cluster analysis detected two plant functional groups: a tropical desert formation and a shrub and dry forest formation. Variation partitioning revealed edaphic variables to be more important in structuring vegetation than mean annual rainfall. Extending irrigation in parts of the study area may possibly be beneficial for local residents. However, it will almost certainly trigger the extinction of the last remnants of the highly endemic tropical dry forest formations.

Zusammenfassung: Tropische Trockenwälder sind die gefährdetsten Ökosysteme der Tropen. Tropische Trockenwälder verfügen über eine außerordentlich hohe Beta-Diversität, welche mit der tropischer Regenwälder vergleichbar ist und doch sind sie immer noch chronisch untererforscht. Darüber hinaus formt die El Niño Southern Oscillation maßgeblich diese einzigartigen und hochendemischen Ökosysteme in Nordperu. Diese Studie soll zeigen, (i) ob die verholzende Pflanzensammensetzung dem Hauptgradienten in diesem per- bis semiariden Gebiet folgte und (ii) welchen Einfluss klimatische und edaphische Faktoren auf die floristische Zusammensetzung ausüben. Wir untersuchten 50 30 × 30 m² zufällig ausgewählte Aufnahmeflächen entlang eines Feuchtegradienten. Ein Natrium-Korngröße-Gradient korrelierte mit der ersten Isomap-Achse. Kalium und pH charakterisierten die zweite Achse und spiegelten hauptsächlich den Feuchtegradienten wider. Eine Cluster-Analyse ergab zwei funktionelle Pflanzengruppen: eine tropische (Halb-)Wüsten Formation und eine Busch-/Trockenwaldformation. Eine Varianzpartitionierung offenbarte, dass edaphische Variablen einen größeren Einfluss auf die Vegetationsstruktur ausüben als der mittlere jährliche Niederschlag. Die Ausweitung bewässerten Kulturlandes in Teilen unseres Studiengebietes wird für die Lokalbevölkerung möglicherweise von Vorteil sein, andererseits aber höchstwahrscheinlich die letzten Überbleibsel der hochendemischen tropischen Trockenwaldformation in unserem Studiengebiet auslöschen.

Keywords: Biogeography, climatic gradient, edaphic gradient, tropical drylands, Isomap ordination, South America

1 Introduction

Dry forests are the most endangered tropical ecosystem (JANZEN 1988) and have their widest distribution in the Neotropical and Caribbean region (MILES et al. 2006). Tropical dry forests are of paramount importance due to distinct characteristics. First, they encompass 42% of all tropical ecosystems (MILES et al. 2006). Thus, they sequester carbon in such a quantity that they might help to mitigate climate change, especially if protected and restored (BECKNELL et al. 2012). Secondly, they are host to disproportionately high endemism, a large variety of functional groups

of plants and animals, and exhibit an outstanding beta diversity (DIRZO and RAVEN 2003). Finally, a remarkable 60% of Neotropical dry forests have already been lost (MILES et al. 2006) and Peru has even converted 95% of its tropical dry forests to other land uses (PORTILLO-QUINTERO and SANCHEZ-AZOFEIFA 2010). It is thus most surprising that tropical research mainly focuses on humid forests (SANCHEZ-AZOFEIFA et al. 2005; MILES et al. 2006). It is even more alarming that most of the available ecological knowledge stems from only a few tropical dry forest sites in Brazil, Costa Rica, Mexico and Puerto Rico (PORTILLO-QUINTERO and SANCHEZ-AZOFEIFA 2010).

Water is most likely the most important limiting abiotic factor in tropical dry forests as it influences plant recruitment, establishment and survival as well as seedling production (BALVANERA et al. 2011). Yet, other variations in the physical environment also affect the vegetation in tropical dry forests (TABARELLI et al. 2003). Generally, studies of gradients are of fundamental importance in biogeographic and ecological research (LOMOLINO 2001; PALIN et al. 2011). Although altitudinal gradients have attracted much scientific attention (RAHBK 2005; BECK et al. 2008), climatic and edaphic gradients are equally important (e.g., POWERS et al. 2009; ESPINOSA et al. 2011). Within tropical dry forest studies, woody vegetation has frequently been related to water availability (e.g., BALVANERA et al. 2002; TABARELLI et al. 2003; ESPINOSA et al. 2011) but also to disturbance (SAGAR et al. 2003), succession (MADEIRA et al. 2009) and edaphic gradients (POWERS et al. 2009; ESPINOSA et al. 2011).

Furthermore, it is especially important to monitor vegetation development in arid to semi-arid regions as they tend to be vulnerable towards degradation caused by local human activity and/or climate change (SIVAKUMAR et al. 2005; WAGENSEIL and SAMIMI 2007; SCHULZ et al. 2011). For instance, NW-Peru is an arid to semi-arid region of extremely high climate variability primarily caused by the El Niño Southern Oscillation (ENSO; MUENCHOW et al. 2013a; MUENCHOW et al. 2013c). Both El Niño (LOPEZ

et al. 2006) and La Niña (MUENCHOW et al. 2013b) heavily influence primary productivity in NW-Peru. Furthermore, grazing, agriculture and urban expansion have strongly changed the floristic composition of tropical dry forests in NW-Peru (EKTVEDT 2011; EKTVEDT et al. 2012). Hence, the last remnants of tropical dry forest in NW-Peru should be a top priority target for conservation planning (MADEIRA et al. 2009).

To assemble comprehensive ecological knowledge of tropical dry forests, SANCHEZ-AZOFEIFA et al. (2005) have proposed to address several key questions. First, common ecological patterns should be identified in less well-studied regions. Secondly, how does species composition change along gradients? Thirdly, in the case of a detectable species turnover, what are the dominant functional groups? To answer these questions, we sampled 50 30×30 m² plots along a climatic gradient in a scientifically neglected region. We aimed to investigate the floristic composition of the woody vegetation, and how it is structured by precipitation and edaphic variables.

2 Study area and methods

2.1 Study site and sampling

The study area stretches from the Pacific coast to the foreland of the Andes near Chulucanas (NW-

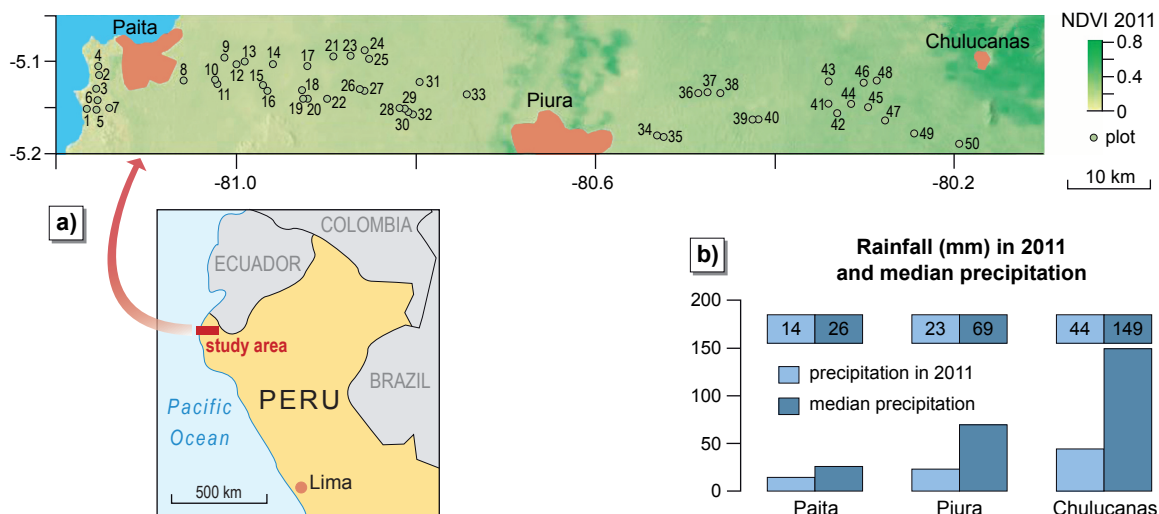


Fig. 1: Characteristics of the study area. a) Location of all sampled plots and the NDVI of April during the study year 2011 (data: MODIS; <https://lpdaac.usgs.gov/>). b) Precipitation barplot for major towns within the study area. Precipitation in 2011 was measured at three automatic climate stations in Cangrejos (near Paita), Piura (Universidad de Piura) and near Chulucanas (close to relevé 46). Median precipitation values were calculated for different time periods: Paita (2005-08; data: Proyecto Chira y Piura), Piura (1991-2011; data: Universidad de Piura), Chulucanas (1942-2008 (missing years: 1969-72, 1991-96); data: Proyecto Chira y Piura)

Peru; Fig. 1a). As a part of the Sechura desert, our study area is characterized by extremely variable annual precipitation (BENDIX 1999). The median precipitation gradient ranges from 29 mm yr⁻¹ (Paita/Cangrejos) in the west to approximately 149 mm yr⁻¹ (Chulucanas, Fig. 1b) in the east; yet interannual variability can be extremely high (RICHTER and ISE 2005; BENDIX et al. 2011; MUENCHOW et al. 2013b). Our study year endured a severe La Niña event (MUENCHOW et al. 2013b) during which precipitation during the rainy season (January to April) was well below the median values (Fig. 1b). Vegetation changes from a tropical desert to a tropical dry forest formation along the precipitation gradient (MUENCHOW et al. 2013b). The precipitation gradient coincides with a land use gradient.

We randomly sampled 50 30 × 30 m² plots along the humidity gradient of our study area (Fig. 1a). Field work was carried out at the end of the rainy season from March to April in 2011. We elaborated a presence-absence matrix of all woody plant species over all plots. Nomenclature follows the Missouri Botanical Garden Tropicos online database (www.tropicos.org). Please refer to MUENCHOW et al. (2013b) for a detailed description of the sampling design.

2.2 Variable assessment

We collected three randomly chosen soil samples in 15 cm and 30 cm depth in each plot and

measured soil pH, electrical conductivity, the carbon-nitrogen ratio, soil texture, P, and cations (Ca, Mg, K, Na; Tab. 1). The coverage of soil (naked soil) was estimated as a percentage in the field, and opposes rock cover. Skeletal content was the gravimetric proportion of stones (> 2 mm; Tab. 1). Please refer to MUENCHOW et al. (2013b) for a detailed description of all soil analyses performed in the laboratory. Annual precipitation values for each plot were derived from the WorldClim dataset (HIJMANS et al. 2005; Tab. 1).

2.3 Statistical analyses

We calculated WHITTAKER'S (1972) diversity indices. Alpha diversity was computed as the mean species number per site, beta diversity as the ratio of the total number of species to the average number of species minus 1. Gamma diversity is simply given as the total number of species along all sampled units.

To analyze the floristic composition, we subjected our data to Isomap ordination. Initially, Isomap computes the number of neighboring points k for a given point. If k is low, a strong non-linear relationship is apparent (FEILHAUER et al. 2011). Secondly, Isomap calculates geodesic distances between sample points with k neighbors based on a distance matrix, in our case Bray-Curtis. This retains essentially the shortest path in

Tab. 1: Descriptive statistics of all environmental variables used in the statistical analyses

Variables and explanation	Unit	Mean	Min	Max
Calcium (Ca)	cmol/kg	8.8	2.2	31.7
Carbon-nitrogen ratio (C/N)	–	10.9	0.0	145.1
Electrical conductivity (ec)	μS	363	19	3650
Magnesium (Mg)	cmol/kg	0.77	0.23	2.2
pH	–	6.83	5.94	7.28
Phosphor (P)	g/kg	7.57	0.00	28.95
Potassium (K)	cmol/kg	0.35	0.08	0.75
Precipitation	mm	66	21	174
Sand content (Sand)	%	81.1	16.7	99.6
Skeletal content	%	15	0.00	72
Sodium (Na)	cmol/kg	0.30	0.24	0.51
Soil cover (cov_soil)	%	87.63	10	100

a curved space. Finally, Isomap subjects the geodesic distance matrix to classical multidimensional scaling (TENENBAUM et al. 2000). We performed Isomap ordination with k ranging between 1 and the sample size minus 1, and chose the ordination with the highest explained variance (FEILHAUER et al. 2011).

To derive cluster classes, we fed the partitioning around medoids (PAM) algorithm a Bray-Curtis-transformed species matrix. PAM estimates medoids of the cluster centers (REYNOLDS et al. 2006). The mean average silhouette width over all clusters indicated an optimal number of cluster classes.

Moreover, we were interested in explaining the floristic gradient using edaphic variables and precipitation. Consequently, we subjected the scores of the first and the second Isomap axis, respectively, to variation partitioning. Variation partitioning aims at detecting the contribution of all subsets of variables to the explained variance while controlling for the effect of the other subsets (BORCARD et al. 1992). We log-transformed electrical conductivity, phosphorus and rock cover prior to variation partitioning to meet assumptions of normality. We only retained variables with a variance inflation factor < 3 ; this led to the exclusion of calcium, phosphorus and skeletal content. We applied a hypothesis-based variable selection procedure until only significant terms remained in the variation partitioning models.

All statistical analyses were conducted in the software package R (R Development Core Team 2013) using its packages BiodiversityR (KINDT and COE 2005), cluster (MAECHLER et al. 2013), labdsv (ROBERTS 2013), lattice (SARKAR 2008) and vegan (OKSANEN et al. 2013).

3 Results

Alpha diversity of woody species per plot ranged between zero and six (mean: 3.4). In total, we identified 15 species from 11 families with species from the legume family (Fabaceae) having 4 species. Consequently, species turnover was intermediate to low (Whittaker's beta: 3.4). *Prosopis pallida* was the most frequent species (72%) followed by *Colicodendron scabridum* (60%), *Acacia macracantha* (50%) and *Encelia canescens* (48%).

The best Isomap solution retained a k of 44. The first two axes explained 74%. Adding one further dimension increased the explained variance

to 87.3%. The lengths \pm SD of the first two axes were 0.86 ± 0.24 and 0.77 ± 0.18 , respectively. The first Isomap axis was related to sodium and soil texture. The second axis correlated with pH and soil cover (Fig. 2). Additionally, Isomap was able to differentiate the two plant formations obtained from the clustering (Fig. 2): a tropical (semi-)desert formation and an open shrub to tropical dry forest formation. *Galvesia limensis* and *Colicodendron scabridum* were indicator species of the (semi-)desert formation and *Acacia macracantha*, *Encelia canescens* and *Cordia lutea* characterized the open shrub to tropical dry forest formation.

Prior to partitioning the variance, hypothesis-based variable selection retained the variables soil texture, potassium and sodium for the first axis, and pH as well as soil cover for the second axis. Variation partitioning revealed not only that soil was more important in explaining the floristic gradient than precipitation (Fig. 3) but also that only the soil fraction (p -value Isomap axis 1: 0.01; p -value Isomap axis 2: 0.009) was significant in accordance with a permutation test.

4 Discussion

Isomap successfully reduced dimensionality while retaining a large portion of the variance. A large k indicates a linear relationship along the main gradient (FEILHAUER et al. 2011) which is also confirmed by the linear assemblage of clustered plant functional groups in ordination space. The first two Isomap axes yielded similar standard deviations. Consequently, both of them contributed equally to the explained variance. The first axis showed a sodium-sand gradient. Sandy soils favor woody species because they enhance water infiltration. Thus they slow down evapotranspiration supporting the faster establishment of a deeper root system (NOY-MEIR 1973; SQUEO et al. 2007; SITTERS et al. 2012). Accordingly, coverage of woody species on coastal sandy plots was almost three times higher than on rocky coastal plots. The second Isomap axis correlated well with pH and potassium. As pH is strongly inversely correlated with precipitation (R: -0.87, p -value < 0.01), the second axis mainly represents the humidity gradient. Higher precipitation leads to more leaching of hydrogen ions, thus pH values decrease with increasing humidity (WAGNER et al. 2011). At the same time, potassium contents increased steadily along the humidity gradient, obviously favoring woody plant growth. Our

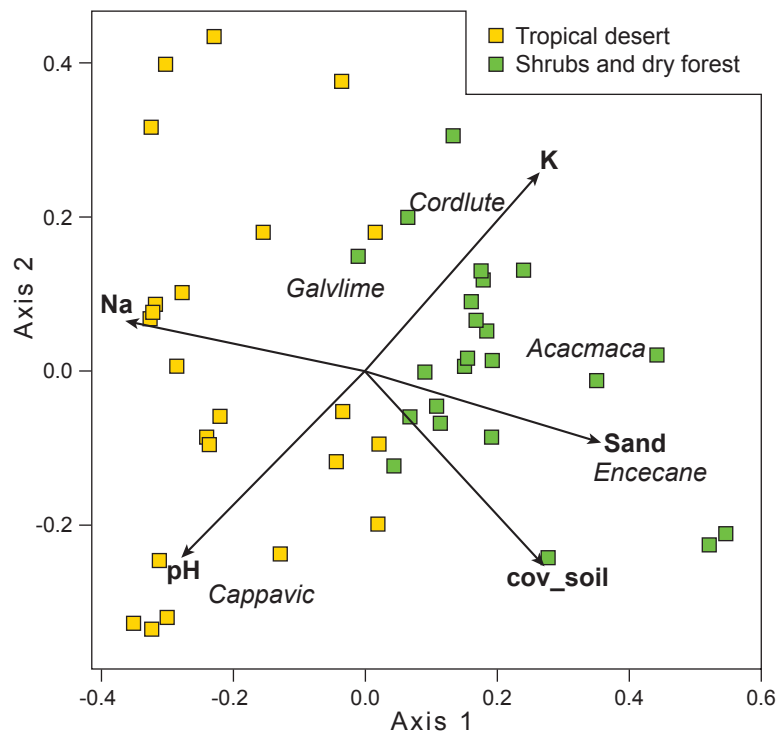


Fig. 2: Isomap ordination plot. Squares refer to the visited plots. Edaphic variables that were rendered significant in the variation partitioning are shown as arrows and indicator species in italics. Vegetation formations correspond to PAM clustering. Abbreviations environmental variables: cov_soil = coverage of soil, K = potassium, Na = sodium. Abbreviations species: *Acacmaca* = *Acacia macracantha* Humb. & Bonpl. ex Willd. (Fabaceae), *Cappavic* = *Capparis avicennifolia* Kunth (Capparaceae), *Cordlute* = *Cordia lutea* Lam. (Boraginaceae), *Encecan* = *Encelia canescens* Cav. (Asteraceae), *Galvlime* = *Galvesia limensis* Domb. ex Benth (Plantaginaceae)

results support the findings of other studies on the species composition of tropical dry forests along edaphic gradients (POWERS et al. 2009; ESPINOSA et al. 2011; PEÑA-CLAROS et al. 2012).

Although water availability is the main limiting abiotic factor in tropical dry forests (ESPINOSA et al. 2011; MUENCHOW et al. 2013b), variation partitioning revealed that edaphic variables were more important than mean annual precipitation in structuring vegetation composition. This seems reasonable, as scattered woody individuals are still present in the hyper-arid environment of the coastal area. RONNENBERG and WESCHE (2011) showed that increasing the precipitation amount alone barely stimulates primary productivity in drylands but that it also requires a certain base-line of nutrient availability (WHITFORD and STEINBERGER 2011). Nevertheless, woody plants of course depend on water availability. Sudden but regular ENSO rain pulses (BENDIX et al. 2011) trigger seedling establishment and expanded tree ring growth (RODRÍGUEZ et al. 2005; LOPEZ et al. 2006). Indeed, SQUEO et al. (2007) showed that the seedlings of *Prosopis pallida*, the most common tree spe-

cies in our study area, survive with only 27 mm of rain in the first year. In the second year, however, *Prosopis pallida* requires at least three times as much water. Thus, two consecutive humid years would enable seedling survival (MUENCHOW et al. 2013b). However, persistent rain scarcity in the coastal area also suggests that already established woody species have access to other water sources such as immeasurable rainfall and fog (MUENCHOW et al. 2013a; MUENCHOW et al. 2013c) or water sources in deeper soil layers (FRAVOLINI et al. 2005). In summary, regular rain pulses in concert with favorable edaphic conditions appear to be more important than mean annual precipitation.

Currently, human activity threatens the unique dry forest formations of NW-Peru which are host to many endemic species. This impact is likely to increase dramatically with the irrigation project Alto Piura (www.peihap.gob.pe). This study provides a baseline for conservation planning of this highly threatened ecosystem.

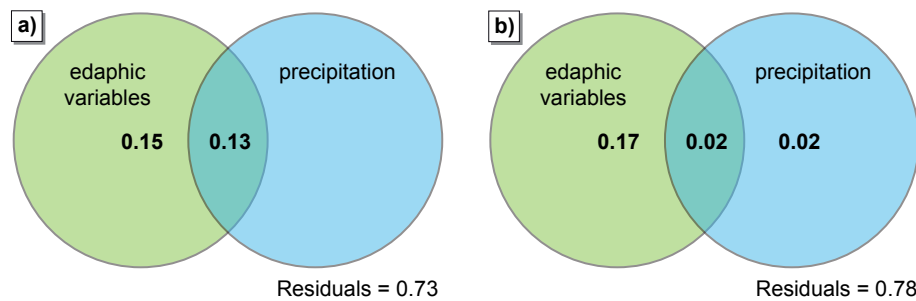


Fig. 3: Variation partitioning of Isomap scores. a) Explaining the first axis with the edaphic covariates (sand, potassium and sodium) and precipitation. b) Explaining the second axis with the edaphic covariates (pH and soil cover). Numbers represent the adjusted coefficient of determination R^2

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References

- BALVANERA, P.; LOTT, E.; SEGURA, G.; SIEBE, C. and ISLAS, A. (2002): Patterns of beta-diversity in a Mexican tropical dry forest. In: *Journal of Vegetation Science* 13, 145–158. DOI: [10.1111/j.1654-1103.2002.tb02034.x](https://doi.org/10.1111/j.1654-1103.2002.tb02034.x)
- BALVANERA, P.; QUIJAS, S. and PEREZ-JIMENEZ, A. (2011): Distribution patterns of tropical dry forest trees along a mesoscale water availability gradient. In: *Biotropica* 43, 414–422. DOI: [10.1111/j.1744-7429.2010.00712.x](https://doi.org/10.1111/j.1744-7429.2010.00712.x)
- BECK, E.; BENDIX, J.; KOTTKE, I.; MAKESCHIN, F. and MOSANDL, R. (eds.) (2008): *Gradients in a tropical mountain ecosystem of Ecuador*. Berlin, Heidelberg.
- BECKNELL, J. M.; KUCEK, L. K. and POWERS, J. S. (2012): Aboveground biomass in mature and secondary seasonally dry tropical forests: A literature review and global synthesis. In: *Forest Ecology and Management* 276, 88–95. DOI: [10.1016/j.foreco.2012.03.033](https://doi.org/10.1016/j.foreco.2012.03.033)
- BENDIX, J. (1999): A comparative analysis of the major El Niño events in Ecuador and Peru over the last two decades. In: *Zentralblatt für Geologie und Paläontologie, Teil I*, 1119–1131.
- 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/erdkunde.2011.02.04](https://doi.org/10.3112/erdkunde.2011.02.04)
- BORCARD, D.; LEGENDRE, P. and DRAPEAU, P. (1992): Partialling out the spatial component of ecological variation. In: *Ecology* 73, 1045–1055. DOI: [10.2307/1940179](https://doi.org/10.2307/1940179)
- DIRZO, R. and RAVEN, P. H. (2003): Global state of biodiversity and loss. In: *Annual Review of Environment and Resources* 28, 137–167. DOI: [10.1146/annurev.energy.28.050302.105532](https://doi.org/10.1146/annurev.energy.28.050302.105532)
- EKTVEDT, T. M. (2011): Firewood consumption amongst poor inhabitants in a semiarid tropical forest: A case study from Piura, northern Peru. In: *Norsk Geografisk Tidsskrift* 65, 28–41. DOI: [10.1080/00291951.2010.549951](https://doi.org/10.1080/00291951.2010.549951)
- EKTVEDT, T. M.; VEETAS, O. and LUNDBERG, A. (2012): Land-cover changes during the past 50 years in the semi-arid tropical forest region of Northern Peru. In: *Erdkunde* 66, 57–75. DOI: [10.3112/erdkunde.2012.01.05](https://doi.org/10.3112/erdkunde.2012.01.05)
- ESPINOSA, C. I.; CABRERA, O.; LUZURIAGA, A. L. and ESCUDERO, A. (2011): What factors affect diversity and species composition of endangered Tumbesian dry forests in Southern Ecuador? In: *Biotropica* 43, 15–22. DOI: [10.1111/j.1744-7429.2010.00665.x](https://doi.org/10.1111/j.1744-7429.2010.00665.x)
- FEILHAUER, H.; FAUDE, U. and SCHMIDTLEIN, S. (2011): Combining Isomap ordination and imaging spectroscopy to map continuous floristic gradients in a heterogeneous landscape. In: *Remote Sensing of Environment* 115, 2513–2524. DOI: [10.1016/j.rse.2011.05.011](https://doi.org/10.1016/j.rse.2011.05.011)
- FRAVOLINI, A.; HULTINE, K. R.; BRUGNOLI, E.; GAZAL, R.; ENGLISH, N. B. and WILLIAMS, D. G. (2005): Precipitation pulse use by an invasive woody legume: the role of soil texture and pulse size. In: *Oecologia* 144, 618–627. DOI: [10.1007/s00442-005-0078-4](https://doi.org/10.1007/s00442-005-0078-4)
- HIJMANS, R. J.; CAMERON, S. E.; PARRA, J. L.; JONES, P. G. and JARVIS, A. (2005): Very high resolution interpolated climate surfaces for global land areas. In: *International Journal of Climatology* 25, 1965–1978. DOI: [10.1002/joc.1276](https://doi.org/10.1002/joc.1276)

- JANZEN, D. (1988): Tropical dry forest: the most endangered tropical ecosystem. In: WILSON, E. (ed.): Biodiversity. Washington, D.C., 130–137.
- KINDT, R. and COE, R. (2005): Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. Nairobi.
- LOMOLINO, M. V. (2001): Elevation gradients of species-density: historical and prospective views. In: Global Ecology and Biogeography 10, 3–13. DOI: [10.1046/j.1466-822x.2001.00229.x](https://doi.org/10.1046/j.1466-822x.2001.00229.x)
- LOPEZ, B. C.; RODRÍGUEZ, R. A.; GRACIA, C. A. and SABATÉ, S. (2006): Climatic signals in growth and its relation to ENSO events of two *Prosopis* species following a latitudinal gradient in South America. In: Global Change Biology 12, 897–906. DOI: [10.1111/j.1365-2486.2006.01138.x](https://doi.org/10.1111/j.1365-2486.2006.01138.x)
- MADEIRA, B.; ESPIRITO-SANTO, M. M.; NETO, S. D.; NUNES, Y. R. F.; AZOFEIFA, G. A. S.; FERNANDES, G. W. and QUEVEDO, M. (2009): Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. In: Plant Ecology 201, 291–304. DOI: [10.1007/s11258-009-9580-9](https://doi.org/10.1007/s11258-009-9580-9)
- MAECHLER, M.; ROUSSEEUW, P.; STRUYF, A.; HUBERT, M. and HORNIK, K. (2013): Package cluster: Cluster analysis basics and extensions. <http://cran.r-project.org/package=cluster> (date: 11.06.2013).
- 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](https://doi.org/10.1111/j.1365-2699.2005.01424.x)
- MUENCHOW, J.; BRÄUNING, A.; RODRÍGUEZ, E. F. and VON WEHRDEN, H. (2013a): Predictive mapping of species richness and plant species' distributions of a Peruvian fog oasis along an altitudinal gradient. In: Biotropica. DOI: [10.1111/btp.12049](https://doi.org/10.1111/btp.12049)
- MUENCHOW, J.; FEILHAUER, H.; BRÄUNING, A.; RODRÍGUEZ, E. F.; BAYER, F.; RODRÍGUEZ, R. A. and VON WEHRDEN, H. (2013b): Coupling ordination techniques and GAM to spatially predict vegetation assemblages along a climatic gradient in an ENSO-affected region of extremely high climate variability. In: Journal of Vegetation Science. DOI: [10.1111/jvs.12038](https://doi.org/10.1111/jvs.12038)
- MUENCHOW, J.; HAUSTEIN, S.; BRÄUNING, A.; BÄUMLER, R.; RODRÍGUEZ, E. F. and VON WEHRDEN, H. (2013c): Soil texture and altitude, respectively, largely determine the altitudinal vegetation zonation of the most diverse fog oasis in the Peruvian desert. In: Journal of Tropical Ecology. DOI: [10.1017/S0266467413000436](https://doi.org/10.1017/S0266467413000436)
- 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](https://doi.org/10.1146/annurev.es.04.110173.000325)
- OKSANEN, J.; BLANCHET, F. G.; KINDT, R.; LEGENDRE, P.; MINCHIN, P.; O'HARA, R. B.; SIMPSON, G. L.; SOLYMOS, P.; STEVENS, M. H. H. and WAGNER, H. (2013): Package vegan: Community ecology package. <http://CRAN.R-project.org/package=vegan> (date: 11.06.2013).
- PALIN, O. F.; EGGLETON, P.; MALHI, Y.; GIRARDIN, C. A. J.; ROZAS-DAVILA, A. and PARR, C. L. (2011): Termite diversity along an Amazon-Andes elevation gradient, Peru. In: Biotropica 43, 100–107. DOI: [10.1111/j.1744-7429.2010.00650.x](https://doi.org/10.1111/j.1744-7429.2010.00650.x)
- PEÑA-CLAROS, M.; POORTER, L.; ALARCON, A.; BLATE, G.; CHOQUE, U.; FREDERICKSEN, T. S.; JUSTINIANO, M. J.; LEANO, C.; LICONA, J. C.; PARIONA, W.; PUTZ, F. E.; QUEVEDO, L. and TOLEDO, M. (2012): Soil effects on forest structure and diversity in a moist and a dry tropical forest. In: Biotropica 44, 276–283. DOI: [10.1111/j.1744-7429.2011.00813.x](https://doi.org/10.1111/j.1744-7429.2011.00813.x)
- PORCILLO-QUINTERO, C. A. and SANCHEZ-AZOFEIFA, G. A. (2010): Extent and conservation of tropical dry forests in the Americas. In: Biological Conservation 143, 144–155. DOI: [10.1016/j.biocon.2009.09.020](https://doi.org/10.1016/j.biocon.2009.09.020)
- POWERS, J. S.; BECKNELL, J. M.; IRVING, J. and PEREZ-AVILES, D. (2009): Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. In: Forest Ecology and Management 258, 959–970. DOI: [10.1016/j.foreco.2008.10.036](https://doi.org/10.1016/j.foreco.2008.10.036)
- R Development Core Team (2013): R: A language and environment for statistical computing. <http://www.R-project.org/> (date: 11.06.2013).
- RAHBEK, C. (2005): The role of spatial scale and the perception of large-scale species-richness patterns. In: Ecology Letters 8, 224–239. DOI: [10.1111/j.1461-0248.2004.00701.x](https://doi.org/10.1111/j.1461-0248.2004.00701.x)
- REYNOLDS, A.; RICHARDS, G.; IGLESIA, B. and RAYWARD-SMITH, V. (2006): Clustering rules: a comparison of partitioning and hierarchical clustering algorithms. In: Journal of Mathematical Modelling and Algorithms 5, 475–504. DOI: [10.1007/s10852-005-9022-1](https://doi.org/10.1007/s10852-005-9022-1)
- RICHTER, M. and ISE, M. (2005): Monitoring plant development after El Niño 1997/98 in northwestern Peru. In: Erdkunde 59, 136–155. DOI: [10.3112/erdkunde.2005.02.05](https://doi.org/10.3112/erdkunde.2005.02.05)
- ROBERTS, D. W. (2013): labdsv: ordination and multivariate analysis for ecology. <http://CRAN.R-project.org/package=labdsv> (date: 12.06.2013).
- RODRÍGUEZ, R. A.; MABRESA, A.; LUCKMAN, B.; EVANS, M.; MASIOKAS, M. and EKTVEDT, T. M. (2005): “El Niño” events recorded in dry-forest species of the lowlands of northwest Peru. In: Dendrochronologia 22, 181–186. DOI: [10.1016/j.dendro.2005.05.002](https://doi.org/10.1016/j.dendro.2005.05.002)
- RONNENBERG, K. and WESCHE, K. (2011): Effects of fertilization and irrigation on productivity, plant nutrient contents and soil nutrients in southern Mongolia. In: Plant and Soil 340, 239–251. DOI: [10.1007/s11104-010-0409-z](https://doi.org/10.1007/s11104-010-0409-z)

- SAGAR, R.; RAGHUBANSHI, A. S. and SINGH, J. S. (2003): Tree species composition, dispersion and diversity along a disturbance gradient in a dry tropical forest region of India. In: *Forest Ecology and Management* 186, 61–71. DOI: [10.1016/s0378-1127\(03\)00235-4](https://doi.org/10.1016/s0378-1127(03)00235-4)
- SANCHEZ-AZOFEIFA, G. A.; QUESADA, M.; RODRIGUEZ, J. P.; NASSAR, J. M.; STONER, K. E.; CASTILLO, A.; GARVIN, T.; ZENT, E. L.; CALVO-ALVARADO, J. C.; KALACSKA, M. E. R.; FAJARDO, L.; GAMON, J. A. and CUEVAS-REYES, P. (2005): Research priorities for neotropical dry forests. In: *Biotropica* 37, 477–485. DOI: [10.1111/j.1744-7429.2005.00066.x](https://doi.org/10.1111/j.1744-7429.2005.00066.x)
- SARKAR, D. (2008): *Lattice: multivariate data visualization with R*. New York.
- SCHULZ, N.; ACEITUNO, P.; RICHTER, M.; 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](https://doi.org/10.3112/erdkunde.2011.02.05)
- SITTEERS, J.; HOLMGREN, M.; STOOBVOGEL, J. J. and LOPEZ, B. C. (2012): Rainfall-tuned management facilitates dry forest recovery. In: *Restoration Ecology* 20, 33–42. DOI: [10.1111/j.1526-100X.2010.00761.x](https://doi.org/10.1111/j.1526-100X.2010.00761.x)
- SIVAKUMAR, M. V.; DAS, H. P. and BRUNINI, O. (2005): Impacts of present and future climate variability and change on agriculture and forestry in the arid and semi-arid tropics. In: *Climatic Change* 70, 31–72. DOI: [10.1007/s10584-005-5937-9](https://doi.org/10.1007/s10584-005-5937-9)
- SQUEO, F. A.; HOLMGREN, M.; JIMENEZ, M.; ALBAN, L.; REYES, J. and GUTIÉRREZ, J. (2007): Tree establishment along an ENSO experimental gradient in the Atacama Desert. In: *Journal of Vegetation Science* 18, 195–202. DOI: [10.1111/j.1654-1103.2007.tb02530.x](https://doi.org/10.1111/j.1654-1103.2007.tb02530.x)
- TABARELLI, M.; VICENTE, A. and BARBOSA, D. C. A. (2003): Variation of seed dispersal spectrum of woody plants across a rainfall gradient in north-eastern Brazil. In: *Journal of Arid Environments* 53, 197–210. DOI: [10.1006/jare.2002.1038](https://doi.org/10.1006/jare.2002.1038)
- TENENBAUM, J. B.; SILVA, V. DE and LANGFORD, J. C. (2000): A global geometric framework for nonlinear dimensionality reduction. In: *Science* 290, 2319–2323.
- WAGENSEIL, H. and SAMIMI, C. (2007): Woody vegetation cover in Namibian savannahs: a modelling approach based on remote sensing. In: *Erdkunde* 61, 325–334. DOI: [10.3112/erdkunde.2007.04.03](https://doi.org/10.3112/erdkunde.2007.04.03)
- WAGNER, V.; VON WEHRDEN, H.; WESCHE, K.; FEDULIN, A.; SIDOROVA, T. and HENSEN, I. (2011): Similar performance in central and range edge populations of a Eurasian steppe grass under different climate and soil pH regimes. In: *Ecography* 34, 498–506. DOI: [10.1111/j.1600-0587.2010.06658.x](https://doi.org/10.1111/j.1600-0587.2010.06658.x)
- WHITFORD, W. G. and STEINBERGER, Y. (2011): Effects of simulated storm sizes and nitrogen on three Chihuahuan Desert perennial herbs and a grass. In: *Journal of Arid Environments* 75, 861–864. DOI: [10.1016/j.jaridenv.2011.03.007](https://doi.org/10.1016/j.jaridenv.2011.03.007)
- WHITTAKER, R. H. (1972): Evolution and measurement of species diversity. In: *Taxon* 21, 213–251. DOI: [10.2307/1218190](https://doi.org/10.2307/1218190)

Authors

Dipl.-Geogr. Jannes Muenchow
 Prof. Dr. Michael Richter
 Institute of Geography
 University of Erlangen-Nuremberg
 Kochstr. 4
 91054 Erlangen
 Germany
jannes.muenchow@fau.de
sairecabur@web.de

Prof. Dr. Henrik von Wehrden
 Institute of Ecology
 Faculty of Sustainability and Center for Methods
 Leuphana University
 Scharnhorststr. 1
 21335 Lüneburg
 Germany
henrik.von_wehrden@leuphana.de

M.Sc. Eric Frank Rodríguez
 Herbarium Truxillense
 National University of Trujillo
 Jr. San Martín 392
 Trujillo
 Peru
erodriguez@unitru.edu.pe

M.Sc. Rodolfo Arisméndiz Rodríguez
 Faculty of Engineering
 University of Piura
 Av. Ramón Murgica 131
 Piura
 Peru
rodolfo.rodriguez@udep.pe

Dipl.-Geogr. Fabian Bayer
 Faculty of Geography
 University of Marburg
 Deutschhausstr. 10
 35032 Marburg
 Germany
bayerfa@staff.uni-marburg.de